Preface

Volume 104 of the Journal for 2021 had 11 contributions of which 5 were full papers, 5 were short Research Notes—a category not used since 2012 in volume 95—and an obituary for Alex Bevan (WA Museum). During 2021 the Society held two symposia: 'Swan Coastal Plain – temporal and spatial patterns' on 15 March, and the inaugural John Glover Symposium on 'The Southwest Biodiversity Hotspot' held on 3–4 September—the latter to honour John's generosity to the Society.

Further symposia planned for 2022 will be announced via the Society's website.

Articles in volume 104 included diverse topics such as snakes from the Banda Arc and plant biodiversity of the Southwest, both of which were originally presented at the Society's 2020 Wallacea symposium. Other larger articles covered: combustion features in Indigenous archaeological sites, a re-evaluation of sea temperature and density measurements made during 1896 off southern Australia, and Lower Permian palynomorphs. The Research Notes consisted of an account of zamia poisoning of crew from the de Vlamingh expedition of 1697, use of fertilizer in the Northern Jarrah Forest, a mud minnow from Ellen Brook, an example of recent avian kleptoparasitism, and the Black-striped Burrowing Snake around Perth. Two of the research notes were from a 19-year old Perth Modern student—probably the Society's youngest contributor since its foundation in 1899.

Future changes to the editorial process for the journal will include greater insistence on following the guide to authors and the employment of external copy editors, which should speed the progression of manuscripts once accepted by the reviewers.

The Editorial Board
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An unidentified word in the account of the zamia poisoning on de Vlamingh's expedition of 1697

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The previously unexplained word '*Drioens*' in the journal entry for de Vlamingh's 1697 excursion near present-day Perth, Western Australia, is recognised as slang spelling of the Dutch name for the Sumatran durian fruit, typically *Durio zibethinus*.

Keywords: de Vlamingh, Dutch exploration, zamia, durian, Drioens

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INTRODUCTION

During his explorations of the west coast of Australia, Willem de Vlamingh, commander of the *Geelvinck, Wesel* and *Nijptangh,* went ashore near Perth in January 1697. He and his men divided into three parties and investigated the area around the Swan River. Among other things, the men were astounded by the rich vegetation. This almost brought a number of them to grief.

The diarist of this expedition, thought to be the upper-surgeon Mandrop Torst (Schilder 1985, p. 13), recorded the following incident:

> Ondertusschen wierd my een pit van een zekere Vrucht aangebooden, van gedaante niet kwalyk gelykende na de *Drioens*, en van smaak na de Vaderlandsche groote Boonen, en, die jonger waren, na een Zinknoot. Ik at'er vyf à ses ... doch na verloop van omtrent drie uuren begon ik, en noch vyf anderen die mede van de gezeide Vruchten gegeeten hadden, zo geweldig te braaken, dat tusschen de dood en ons naauwelycks onderscheid was.
>
> (In the meantime I was offered the kernel of a certain fruit not unlike the *Drioens* in appearance, and tasting like our Dutch broad beans and those which were less ripe, like a hazelnut. I ate five or six ... but after an interval of about three hours I and five more of the others who had also eaten of the said fruit began to vomit so violently that there was hardly any distinction between death and us.) (Torst 1701, p. 15; Schilder 1985, p. 155).

The men had eaten the poisonous kernels of the zamia (*Macrozamia riedlei*).

The statement that the kernels appeared in shape 'not unlike the *Drioens*' has been an interpretative difficulty for scholars since the nineteenth century. Modern scholars have not identified the word 'Drioens'. In the first edition of 1701 the word is both capitalised and italicised (as '*Drioens*'). In this edition, place names and nouns such as beans and hazelnut are usually capitalised but not italicised (as 'Boonen', 'Zinknoot'). The only other word that is, like 'Drioens', both capitalised and italicised, is '*Lignum Rhodii*', a type of balm. A nineteenth century English translator (Major 1859, p. 123) suggested in a footnote that *Drioens* might have been a misspelling of some other word as it did 'not occur in Nemnich's polyglot *Lexikon der Naturgeschichte*', which was published in four volumes from 1793–1798 in Leipzig. The editor of the standard modern edition of the voyage commented as follows: '*Drioens*: an inexplicable name; the kernel mentioned is the nut of the Zamia palm' (Schilder 1985, p. 241).

DISCUSSION

There is a solution to this problem. The word *Drioens* in the expedition diary is found in other early eighteenth century Dutch work about the East Indies. In a treatise on the natural history of the islands of Ambon, Banda, Timor, Celebes, and Bali, François Valentyn (1726, p. 158) made the following important observation:

> Onder de Vrugt-boomen kenne ik'er geen, die zoo hoog, en zoo regt op wascht, als de Doerian-boom, by de onkundige gemeenelyk de Drioens-boom genaamd.
>
> (Among the fruit-trees I know of none that grow as tall and as straight as the Durian tree, commonly called the 'Drioens tree' by the ignorant.)

It appears then that Drioens is a slang spelling for Doerian, the name of the Durian tree. This slang spelling of Drioens for Doerian can be found in other Dutch writings associated with the East India Company. In the old songbook *De Oost-Indische Theeboom* (The East Indian Tea tree), published in 1767 in Amsterdam, there is a drinking song entitled 'Een Nieuw Oost-Indies Lied. Stem: a koele Wei! o derre Hei' that lists the Drioen alongside other fruits. The song describes travelling the route to 'Jakrata':

> 'Zag schoone Boomen staan,
> Met haar vrugten aangenaam,
> Klappers, Pisank.
> Ook Arak tot Pinank
> Annasse, Soorsak en Drioen'
>
> (I saw beautiful trees standing,
> pleasant with their fruits,
> coconut, banana.
> Also areca nut palm [betel],
> pineapples, soursop and durian).

The translation of the song has been made by considering rare words for trees used by the Dutch in the East Indies, some of which are mentioned in Stavorinus (1798), Kalff (1927) and Madhi (2007).

The spelling of the durian in the 1767 songbook is Drioen. However, an older version of the same songbook has yet another variant in the line reading 'Anaffe Soofach, en Drieoen' (Graaf 1716), showing fluidity in spelling of these common fruits, as noted already by Madhi (2007). In discussing the song, Kalff (1927) observed that tropical fruits of the region were known under various mixes of Malay, Javanese, and Dutch spelling. There are also other examples of such variations including 'Drieoen'. De Bucquoy (1744, p. 89), writing of his travels in the East Indies, mentioned the 'Drieoen', with the footnote:

> Drieoen, is een Boomvrugt, welke van binnen pitten heest, die vry heet en versterkend van smaak zyn, doch niet zeer aangenaam.
>
> (Drieoen is a treefruit, which has kernels on the inside, which are hot and invigorating in taste, but not very pleasant).

Traditionally, durian seeds in the region have long been roasted, boiled, or fried in oil (Ho & Bhat, 2015).

The Dutch physician Wouter Schouten, in his popular travel book of his journeys to the East Indies but in the latter half of the seventeenth century (Schouten 1676), wrote that the durian was called by the bastardized name Dryuns or they spoke of 'stinkers'. The edible durian, famous for its strong odour and thorny rind, would have been known to de Vlamingh, who was on his third voyage to the East Indies, and to those of his men who had sailed in this region before.

William Dampier also described the durian in 1697, noting that 'within the fruit there is a stone as big as a small bean' (Dampier 1699, p. 319–320). Yule and Burnell (1886, p. 255), in a glossary of Indian and Indies words, describe the 'dorian in Sumatra' and say that 'the offensive odour of the fruit … procured for it the inelegant Dutch nickname of *stancker*.' Stavorinus (1798, p. 198), in his book on his travels to Batavia, described how the 'Durioens, of Drioens-boom' ('Durian-tree, or Drioens-tree'), was offensive to the smell but had 'a strong invigorating force', and noted that it was considered a strong stimulant and 'therefore much prized by the Chinese'; the English translation includes in a footnote (p. 236) that 'Dr Thunberg says, it is considered as diuretic, and sudorific, and serviceable in expelling wind.' Ho and Bhat (2015) noted that durian was traditionally used in Indonesia and Malaysia as an antipyretic, and to treat jaundice and skin problems. These beliefs might explain why Torst, the surgeon, had *Drioens* in italics as for another medicinal plant, *Lignum.*

The word Drioens was also in maritime use in de Vlamingh's time, with the Straat of Drioens named by the Dutch East India Company in the 1600s (Ormeling 2010). It lies to the east off Sumatra and is strewn with islands. Elisa Netscher, who spent most of his life in Sumatra, and was a linguist, historian, and botanist of the region, wrote of the 'straat Doerie of Drioen' (Doerie or Drioen strait) between the Boelang Archipel (now Pulau Bulan) and the Kerimata group (now Karimata Islands; Netscher 1854, p. 115), and described 'Straat Drioen' (Netscher 1870, p. 100). A 1799 map in the National Archives of Singapore, by the English navigators Capt. John Hall of the *Worcester*, Capt. J. Lindsey, Capt. Elmore and others, shows the Strait of Drions, now anglicised from the Dutch Drioens. The Drioens are a suite of islands then known to the British as the Drions, with Great Drion, Little Drion, and False Drion. A Dutch map of 1820 shows the name as Straat Doerian (Nationaal Archief Holland 1820). The islands are now known as the Durians and the strait called Selat Durian in Bahasa Indonesian.

Whereas the word *Drioens* has baffled modern scholarship, the name would have been known to Dutch seamen who sailed the spice routes to the East Indies in the 1600s and 1700s. Fresh fruit was of great importance to men arriving in port after the long voyage—scurvy was rife and deadly. That de Vlamingh's crew had shown little caution and readily consumed a new fresh fruit in a strange land is explained by the similar appearance of the zamia's kernels to the nuts of the durian. Torst's 1697 description of the similarity between durian and zamia is keenly accurate: the seeds of the durian look very much like the kernels of the zamia in shape. The likeness must have suggested to them that this unfamiliar plant was related to the durian and likely edible. That they tasted like hazelnuts, when the durian flesh tastes like almonds to many people, encouraged them to eat more than one.

CONCLUSION

The linguistic evidence presented here shows that the word '*Drioens*' in the journal entry for de Vlamingh's 1697 expedition is a slang spelling of the Dutch name of the Sumatran fruit known as the durian, commonly *Durio zibethinus,* and other *Durio* species.

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Seeing the forest for the trees: fertiliser increases tree growth but decreases understorey diversity in the Northern Jarrah Forest, southwest Australia

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Forestry science and practice suggests thinning and fertiliser increase the growth rates of individual trees. In a recent paper reporting on a long-term experiment in the Northern Jarrah Forest, Bhandari *et al*. (2021) found positive effects of both thinning and fertilisation, and suggested these management practices will result in a shorter return interval for large trees within the population, thereby providing significant benefits at an ecosystem scale. We argue that whereas thinning alone may be beneficial, the application of fertiliser to native ecosystems within the South West Australian Floristic Region requires caution due to impacts on understorey plant diversity. Not only are soils in this region generally deeply-weathered and highly nutrient-deficient, but the evolution of a suite of adaptations for nutrient-acquisition is implicated in both speciation and the maintenance of plant species diversity. Furthermore, long-term experiments in restored jarrah forest indicate that fertiliser both reduces species diversity and increases fine fuel loads. Therefore thinning, but not fertiliser application, is an appropriate management strategy to improve tree growth in this global biodiversity hotspot.

Keywords: diversity; *Eucalyptus*; nutrients; phosphorus; thinning

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INTRODUCTION

A key motivation within silviculture is to maximise plant productivity and tree growth by applying a range of management strategies such as stand thinning. Bhandari *et al*.'s (2021) study on a long-term, large-scale experiment demonstrates the sustained benefits of stand thinning on jarrah (*Eucalyptus marginata*) tree growth. Their study builds on a significant body of knowledge on Northern Jarrah Forest (hereafter jarrah forest) silviculture developed from studies of forest re-growth post-logging (e.g. Abbott & Loneragan 1986 and references therein; Stoneman *et al*. 1997) and newly established stands in areas cleared for bauxite mining (e.g. Grigg & Grant 2009). Bhandari *et al*. (2021) also demonstrate, consistent with previous findings (e.g. Stoneman *et al*. 1997; Grigg & Grant 2009), that thinned jarrah stands exhibit a growth response to fertiliser, unlike dense jarrah stands, presumably because growth of the latter is more constrained by water than by nutrient availability. These studies suggest the combination of thinning and fertiliser application will result, over time, in a greater number of large trees per unit area of jarrah forest. However, there is increasing evidence that applying fertiliser, especially phosphorus (P) for jarrah and eucalypt forest restoration, reduces floristic diversity, alters plant community structure and may increase fire fuel loads (Daws *et al*. 2013, 2015, 2019a, b; Grant *et al*. 2007; Spain *et al*. 2015; Standish *et al*. 2008; Tibbett *et al*. 2019, 2020). Consequently, we argue that Bhandari *et al*. (2021) have missed critical aspects of the ecology of the jarrah forest, particularly the well-recognised drawbacks of fertiliser application.

JARRAH FOREST ECOLOGY

The jarrah forest on the Darling Range of south-west Western Australia contains tall eucalypts dominated by jarrah, with *Corymbia calophylla* as a sub-dominant (Fig. 1). Unique among vegetation types in Mediterranean climates, the forest contains especially tall jarrah (up to 40 m) trees. Jarrah attains these heights due to its deep root system (up to 40 m; Abbott & Loneragan 1986) enabling access to water stored within the deep, highly weathered regolith. Some trees die due to competition for water, and their pursuit of nutrients and water is more important than any contest for light (Cowling *et al*. 1996). The canopy in the jarrah forest is comparatively open with projective cover rarely exceeding 50% (Abbott 1984) and self-thinning is slow (Stoneman *et al*. 1989).

Remarkable plant diversity on severely phosphorus-impoverished soils

A feature of the ancient deeply weathered nature of the landscape within the South West Australian Floristic Region, including the jarrah forest, is that soil nutrient concentrations, including P, are exceptionally low (Lambers *et al*. 2018; Tibbett *et al*. 2020). Understorey

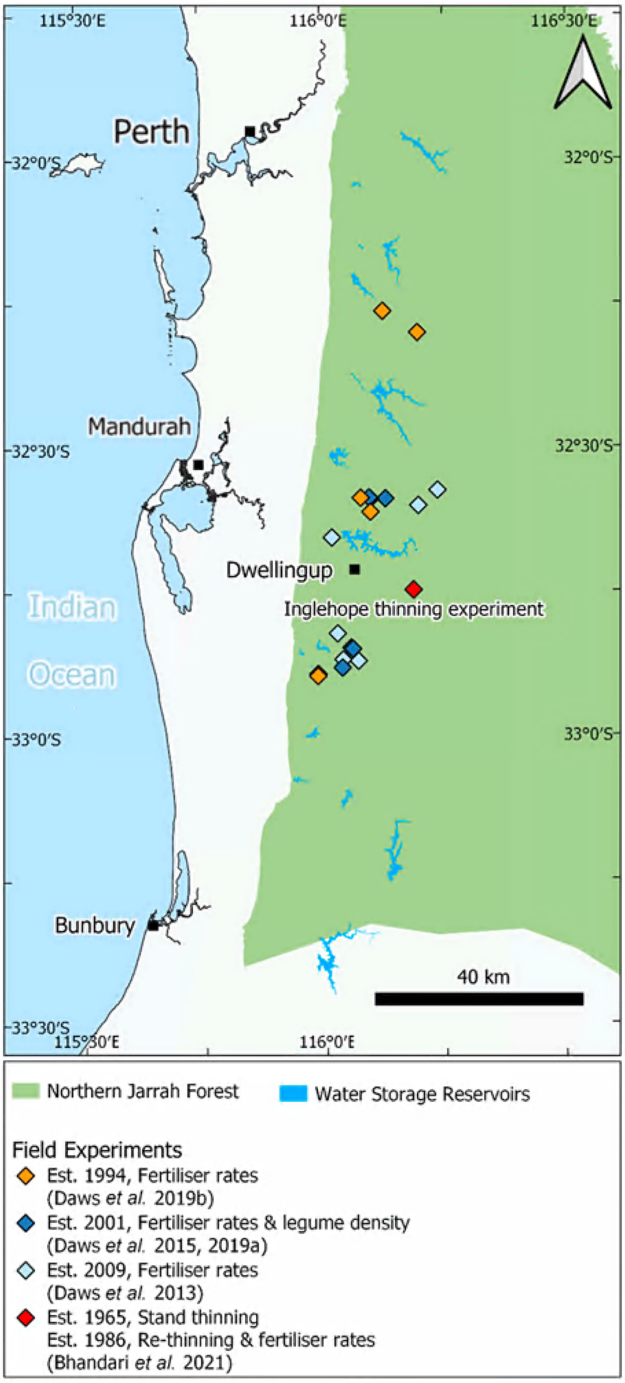
115°30'E
116°0'E
116°30'E
Perth
32°0'S
Mandurah
32°30'S
Dwellingup
Inglehope thinning experiment
Indian
Ocean
33°0'S
Bunbury
40 km
33°30'S
115°30'E
116°0'E
Northern Jarrah Forest
Water Storage Reservoirs
Field Experiments
Est. 1994, Fertiliser rates (Daws et al. 2019b)
Est. 2001, Fertiliser rates & legume density (Daws et al. 2015, 2019a)
Est. 2009, Fertiliser rates (Daws et al. 2013)
Est. 1965, Stand thinning
Est. 1986, Re-thinning & fertiliser rates (Bhandari et al. 2021)

Figure 1. The location of the Inglehope thinning experiment (Bhandari *et al*. 2021) as well as a range of experiments investigating fertiliser application to restored jarrah forest.

diversity is high, with 400–600 species per km^2 in the jarrah forest (Williams & Mitchell 2003). One factor that may have driven speciation and the maintenance of species diversity in this region is the suite of adaptations that species have evolved to enable growth given such low P concentrations (Lambers *et al*. 2018; Sander & Wardell-Johnson 2011). These adaptations for nutrient and P-acquisition include cluster roots, mycorrhizal symbioses and exudation of carboxylates and phosphatases (Lambers *et al*. 2008, 2018). However, many species are unable to down-regulate their P-uptake capacity when P is applied at concentrations just above the natural range in soils and display symptoms of P-toxicity including leaf necrosis and plant death (Shane *et al*. 2004).

Returning large trees

From 1820 to the early 1900s, the jarrah forest produced sawlog-quality trees of 150 cm diameter at breast height over bark (DBHOB) on an estimated rotation of 800–1000 years. However, almost all high-quality stands were logged prior to 1919, and most of the current forest has been cut two to three times (Abbott & Loneragan 1986). This history has largely transformed the jarrah forest from being dominated by a small number of widely spaced, large-diameter trees to a regrowth forest with relatively higher densities of small-diameter trees (Havel *et al*. 1989). The rapid return of large trees with old growth features has tangible economic benefits, given the logging legacy throughout the jarrah forest. There are few large old trees and many stumps. Tree hollows characteristic of large trees provide critical nesting habitat for threatened fauna such as black cockatoos. Assessing the implications of their findings, Bhandari *et al*. (2021) state that:

> Large sized trees resulting from thinning and fertilizer application are likely to provide a greater volume of timber, forage and habitat for arboreal fauna and birds including threatened cockatoos, and more visually appealing forests.

Assuming the annual diameter growth increments reported by Bhandari *et al*. (2021) are maintained, their data suggest that the time to grow poles of 30 cm diameter at breast height under bark (DBHUB) into trees with a DBHUB of 80 cm (the average size of nest trees for threatened black cockatoos; Johnstone *et al*. 2013) is approximately 67 years for heavily thinned and fertilised stands, compared with 625 years for unfertilised stands not subject to thinning. However, applying fertiliser in combination with thinning only reduces this time frame to 51 years, so the growth benefits of thinning and fertiliser application (Bhandari *et al*. 2021) were almost entirely due to thinning. Nonetheless, this largely thinning-driven reduction in the time required to grow trees of >80 cm DBHOB is a significant finding and could potentially make a difference to black cockatoo conservation (Bhandari *et al*. 2021), although the process of hollow formation likely reflects both time and tree age rather than simply being a function of tree size (Stoneman *et al*. 1997). For example, the lowest average age of nest trees recorded for local parrot species is 275 years, and 446 years for local threatened cockatoo species (Mawson & Long 1994).

EVOLVING BEST PRACTICE: THINNING AND FERTILISER APPLICATION

Multiple benefits may accrue from thinning in the jarrah forest. These include:

1) increased growth rates and hence timber production of retained trees (Stoneman *et al*. 1997; Bhandari *et al*. 2021);

2) reduced water use by thinned stands resulting in retained trees being more resilient to a drying climate (Grant *et al*. 2013);

3) reduced water use maintaining ground water levels and stream flows in the face of a drying climate (MacFarlane *et al*. 2010);

4) an increase in inflows to public drinking water dams (MacFarlane *et al*. 2010); and

5) more rapidly setting thinned stands on a trajectory towards developing large trees, and a structure more similar to that in old-growth stands prior to European settlement and logging (pre-1820; MacFarlane *et al*. 2010; Bhandari *et al*. 2021). Perhaps this latter benefit is what Bhandari *et al* (2021) meant by 'more visually appealing forests'.

We suggest there are significant downsides associated with applying fertiliser. The earliest fertiliser research focused on the response of jarrah in the context of maximising timber production (e.g. Abbott & Loneragan 1986). The wider impacts of fertiliser on forest dynamics were not considered until jarrah forest restoration started in earnest in the 1980s (Fig. 1). Whereas fertiliser does increase tree growth in thinned stands, it is necessary to assess what impacts this strategy may have on the diverse and unique understorey flora species of the jarrah forest, many of which are long-lived and slow-growing with specialised adaptations for P-acquisition (Fig. 2). Research suggests a cautious approach to using P fertiliser in inherently P-impoverished systems is warranted. Research includes negative impacts on both native fungal communities (Hilton *et al*. 1989) and understorey diversity in jarrah forest restored after bauxite mining (e.g. Daws *et al*. 2013, 2015, 2019a; Tibbett *et al*. 2020). Moreover, the persistence of fertiliser P in jarrah forest soils after a single application potentially affects vegetation dynamics for decades thereafter (Daws *et al*. 2019b; Standish *et al*. 2008). These findings are consistent with those for P-impoverished systems

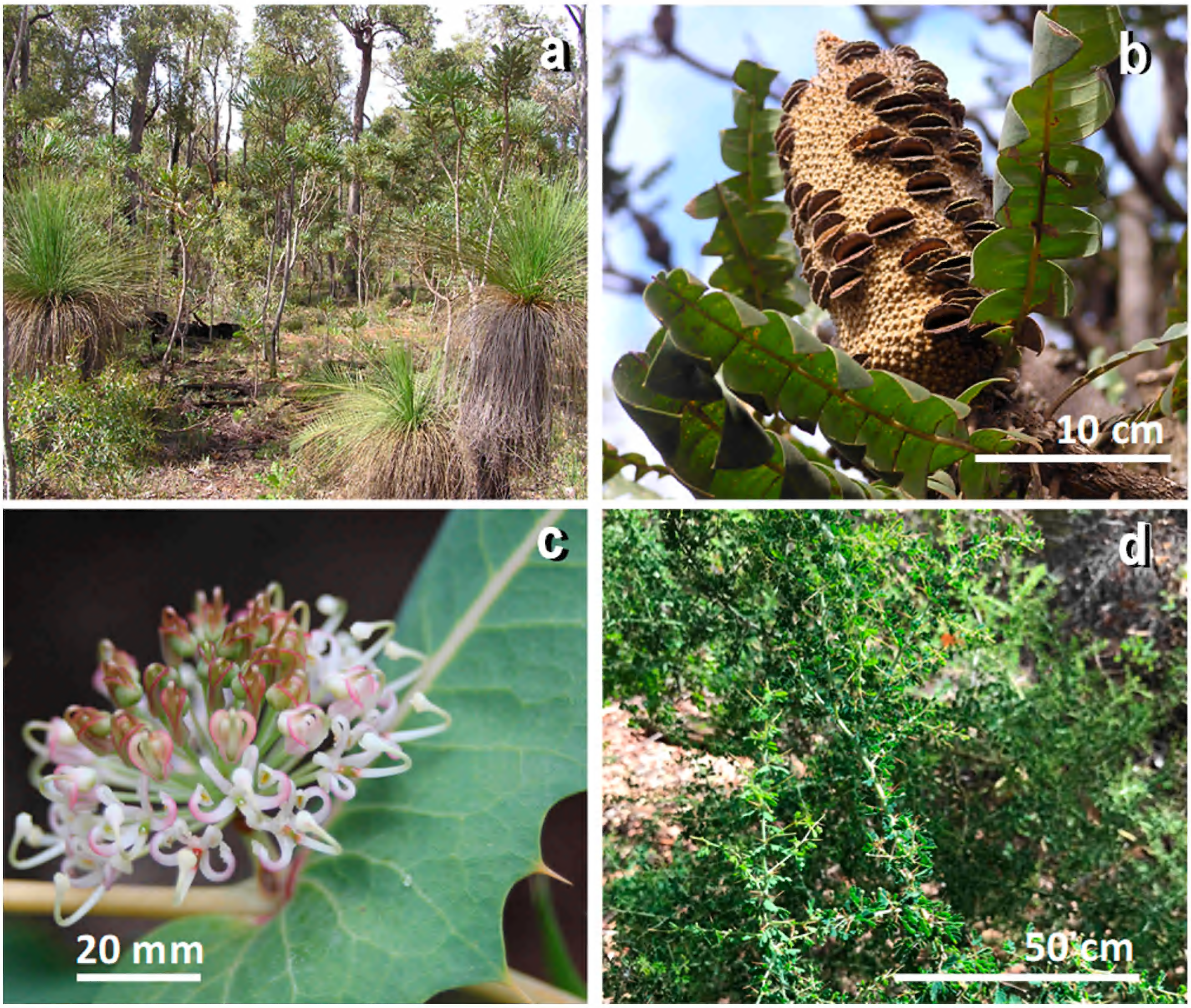

Figure 2. a) An example of the diverse understorey layer in the jarrah forest; b, c) *Banksia grandis* and *Hakea amplexicaulis*, respectively—two species that are sensitive to elevated soil phosphorus concentrations; and d) *Acacia pulchella* a legume that exhibits a vigorous growth response to applied P. Photo credits: a) & b) RJS; c) & d) MID.

elsewhere in the region (e.g. Lambers *et al*. 2018), and declining species diversity in a range of global studies of nutrient effects on nutrient-limited ecosystems (e.g. Ceulemans *et al*. 2014; Isbell *et al*. 2013; Wassen *et al*. 2005). Multiple short- (<5 years) and long-term (20 years) studies of jarrah forest restoration unequivocally demonstrated that adding fertiliser, especially P, reduces understorey species diversity and alters community composition by stimulating the growth of some highly P-responsive, N_2-fixing legume species which outcompete slower-growing species (Daws *et al*. 2013, 2015, 2019a, b; Standish *et al*. 2008; Tibbett *et al*. 2020) and increase fine fuel loads in the understorey (Daws *et al*. 2019a).

The understorey responses to applied fertiliser have not been assessed in the experiment reported by Bhandari *et al*. (2021). Consequently, we believe that this study presents a unique opportunity to further inform this debate, by enabling assessment of long-term fertiliser impacts on the understorey community in the severely nutrient-impoverished environment of the jarrah forest.

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Many words for fire: an etymological and micromorphological consideration of combustion features in Indigenous archaeological sites of Western Australia

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Abstract

The word 'fire' encompasses an enormous variety of human activities and has diverse cultural meanings. The word *hearth* not only has links with fire but also has a social focus both in its Latin origins and in Australian Indigenous languages, where hearth fire is primary to all other anthropogenic fires. The importance of fire to First Nations people is reflected in the rich vocabulary of associated words, from different hearth types and fuel to the different purposes of fire in relation to cooking, medicine, ritual or management of the environment. Likewise, the archaeological expression of hearths and other combustion features is equally complex and nuanced, and can be explored on a microscale using micromorphology. Here we highlight the complexity in both language and micromorphological expressions around a range of documented and less well documented combustion features, including examples from archaeological sites in Western Australia. Our purpose is to discourage the over-use of the generalised term 'hearth' to describe charcoal and ash-rich features, and encourage a more nuanced study of the burnt record in a cultural context.

Keywords: fire, hearth, micromorphology, language, Australia

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BACKGROUND

> '*The hearth fire defined the human world…*' (Pyne 1991, p. 91)

Australia is a continent that burns regularly and in which burned or blackened features are common within archaeological sites. Such features, with or without macroscopic charcoal, are often interpreted as deriving from hearths or the remains of campfires. Whereas the term 'hearth' generally refers to in situ and intact combustion features, less intact blackened, carbonised or ashy features cannot be assumed to be undisturbed or have a cultural origin, or even to be a result of burning (Mentzer 2014; McNiven *et al*. 2018). In the Scopus database the combination of the keywords 'hearth', 'Australia' and 'archaeology' return 23 results but replacing hearth with 'combustion feature' returns only two (Wood *et al*. 2016; Whitau *et al*. 2018) indicating a default interpretation of an in situ cultural hearth. However, there is significant fire-science literature that makes it clear that not all fire is the same (e.g. Pyne 1991; Bowman *et al*. 2011; Scott *et al*. 2014; Tulua 2015) and ethnographic and archaeological literature that similarly indicates great variability in the archaeological traces of hearths (Friesem 2018; Mallol *et al*. 2007, 2017; March *et al*. 2014; Alperson-Afil 2017). The latter are influenced by the function, form and size of the hearth and by the post-depositional processes (e.g. age, soil chemistry, bioturbation) that preserves them (Holdaway *et al*. 2017).

First Nations people in Australia use fire in many ways, and various words in Aboriginal and Torres Strait Islander languages correspondingly describe different types of fire, its behaviour and effects, and also relationships of people with it. In Noongar, the Aboriginal language of southern Western Australia, the word for fire *karl/kaarla* and is the same word for immediate family; similarly *karluk/karlup* means 'place of fire or hearth' (figurative) but also 'home or heart country' (Kelly 1998), a focus mirrored elsewhere around the country. Interestingly, terminology explaining fire as a social focus mirrors the Latin definition of 'focus' which literally means hearth or fireplace. In fact, Pyne (1991, p. 91) denoted the hearth fire as the 'original' of all other anthropogenic fires to the extent that 'without it human society was unthinkable'.

There is also language associated with different types of hearths, such as earth or ground (dug) ovens, which are known variously as *ilda* by Yura Yakarti people in the Flinders Ranges of South Australia (Tunbridge 1985), *kup murri/kup maurior* by Torres Strait Islander (Monaghan 2007; Mua 2018) [i] and also *yulh-tha* by some Cape York people (Alpher 1991), and as *mirnyongs* in eastern and south-eastern Australia (Chauncy 1878, p. 232; Fig. 1).

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[i] See also https://indigenousx.com.au/prioritise-indigenous-knowledges-and-embed-a-western-science-perspective/

Earth ovens may be further distinguished by the different heat retaining elements used and may be differentiated again from rock-filled pit-hearths (Fanning & Holdaway 2001; Wallis *et al*. 2004; Rhodes *et al*. 2009) or surface fires. The Yindjibarndi people of the Pilbara accordingly have different words for a stone hearth *mirin* and a shallow pit fire *yuwarta* (Wordick 1982). More broadly, there is a distinction in language and purpose around fire and hearths.

Fire was not only used for cooking food (*dookerniny* in Noongar (Douglass 1996), *kampa* in Yindjibarndi (Wordick 1982)). Other purposes include warmth (including fires around the camp bed; Douglas 1988), for light (*nyurnmatjali;* Western Desert (Douglass 1988) and *lorrn;* Cape York (Alpher 1991)), hunting (e.g. Bird *et al*. 2008), signalling (e.g. Gould 1971, p. 20; Musharbash 2018), medicine (smoking; e.g. Kelly 1998; Musharbash 2018) and ceremony, including the peacemaking 'fire ceremony' (see Morton nd and references therein). There is also caring-for-country fire (e.g. Hallam 1975; Dortch 2005; Lloyd & Krasnostein 2006), with a similarly rich terminology as Hopper (2019, p. 8) outlined for Noongar:

> Country and various stages in the burning cycle are named firstly *bokyt*—covered in vegetation yet to be burnt—from *bwoka*, the kangaroo skin covering or cloak used for warmth in winter. Then there is *narrik* (dry country ready to burn), *narrow* (to burn slightly), *naariny, naarinj* (burning), *naaranany* (keep burning), *nappal* (burned ground over which fire has passed), and *kundyl* (young grass coming up after fire).

The complex human-fire–environmental relationship acknowledged through language can reveal much about purpose. How fire manifests archaeologically is equally complex and relates not only to the way fire was used but also to how it is preserved and recognised archaeologically (Goldberg *et al*. 2017).

One way to characterise and interpret combustion features in the archaeological record is through micromorphology—a technique that reveals indicators of fire such as char, ash, bone, organic residues and heat-altered sediment in context with sedimentary fabrics characteristics of depositional and environmental processes (Mallol *et al*. 2017; Mentzer 2017). Micromorphology has been used to discriminate surface fires from ground ovens (e.g. Aldeias *et al*. 2016; Haaland *et al*. 2017; Whitau *et al*. 2018), single or multiple hearth use (e.g. Meignen *et al*. 2007), and hearths from secondary ash dumps (e.g. Schiegl *et al*. 2003; Friesem *et al*. 2014). However, with few exceptions (Whitau *et al*. 2018), micromorphology is still largely underused in describing combustion features in Australia.

Focusing mainly on Western Australia, we explore some etymological and micromorphological differences in expression and purpose of combustion features, and in particular in situ hearths, drawing on a range of published and unpublished archaeological sites and language sources. We use Alperson-Alfil's (2017) definition of a hearth as 'an anthropogenic combustion area variable in structure, size, and depth that preserves the remains of burned materials'. It should be noted that two of the micromorphological examples of combustion features presented in this paper were obtained opportunistically from sites sampled during contractual work and one as part of a dedicated research study on Barrow Island off northwestern Australia (Fig. 1). The main purpose of our discussion, which follows others in the same vein (e.g. Aldeias *et al*. 2016; Aldeias 2017; Mentzer 2014), is to highlight the complexity around combustion features as observed in archaeological excavation, and discourage the indiscriminate and inaccurate use of the term hearth to describe these in Australian archaeological discourses. We hope to encourage more studies in Australia to apply geoarchaeological, experimental and ethnoarchaeological methodologies to the study of fire and pyrotechnology to enrich our understanding of the past.

COMBUSTION FEATURES AND THEIR MICROMORPHOLOGICAL CHARACTERISATION

There have been numerous studies on indigenous 'hearth' features in Australia. These are typically regional in aspect (e.g. Beveridge 1869; Wallis *et al*. 2004; Martin 2006; Holdaway *et al*. 2017), with those in and around the Murray Darling (Riverina) area drawing particular attention to mound ovens (Berryman & Frankel 1984; Williams 1985). Other studies explore methods for identifying hearths and their proxies (e.g. burnt bones, charcoal, ash) from geophysical (e.g. Ross *et al*. 2019), chemical (e.g. Singh *et al*. 1991), chronological (e.g. Walshe 2012; Fanning & Holdaway 2001), microscopic techniques (e.g. Whitau *et al*. 2018) and through archaeological experimentation (e.g. Campanelli *et al*. 2018). Other published literature relates to Indigenous language around fire and hearths (Evans 1992; Musharbash 2018). Here we describe different types of combustion features, not all of which can be described as hearths, and how both language and micromorphology might further aid understanding.

Indigenous earth ovens

Indigenous earth ovens—also described as ground ovens, pit oven, heat-retainer oven or hearth—essentially describe those that are dug into the ground, which in profile may intersect an earlier surface. Such ground ovens may be dug over and reformed many times so that intact pits and combustion features may not be common. These may be formed into 'oven mounds' or 'ash hills' (Pyne 1991, p. 89; Ross *et al*. 2019)—in areas with high rainfall and poorly drained soils such mounds may be further repurposed as camping areas or as foundations for huts (Williams 1985). Small mounds bearing fire residues could therefore signify an oven or the remains of a burnt down hut.

Citing Tunbridge (1985), Walsh (2012) described how earth ovens were made by burning wood in a dug hole to form 'coals' (i.e. biochar), to which the food is added and then sealed with hot ash and more 'coals'. Sometimes vegetation is also put into the hole and water poured over the coals to create a steaming effect before sealing.[ii] Rocks were occasionally added, but these had been described ethnohistorically as dangerous due to their 'propensity to explode and embed ... in someone's flesh' (Tunbridge 1985, p. 19). An early account of 'Aboriginal Ovens' by Peter Beveridge (1869) described how baked clay—earth nodules 'baked into the consistency of brick [*sic.*]'—is used if stones were not readily available (see also Martin 2011 and references therein). The hot clay is removed by a pair of 'aboriginal tongs [*sic.*]', after which the hole is carefully swept out, and then lined with damp grass into which the food (often meat) is placed. The oven is sealed with more damp grass and covered with hot clay and fine earth, but never ash. Once the meat is cooked, the covering is scraped off, and the residues (heat-altered clay, ashes, and earth) becomes the nucleus of subsequent earth ovens.

[ii] A similar process, which also uses bark to cover the oven, is also described by the BarengiGadjin people in Victoria: see https://www.youtube.com/watch?v=m-hBCVrk4LQ

As implied from the term, a heat-retainer oven involves the use of heating elements, including lumps from termite nests (e.g. *Drepanotermes perniger*), baked earth (clay), calcrete nodules, stones, charcoal (a man-made product) or coals (a natural mineral; Coutts *et al*. 1979; Berryman & Frankel 1984). Each of these have different cultural terms. In the Yindjibarndi language of the Pilbara, *yawan* is the word for cooking stone (Wordick 1982). In Noongar, charcoal is *kop*, coals *bridal* and white ash *yoort*; and in the Yir-Yiront lexicon of Cape York, distinction is made between hot ashes *thum-nhaq* and cold ashes *thum-nhur* (Alpher 1991). Each of these elements may have different micromophological expression (Mentzer 2017). Villagran *et al*. (2019), for example, used micromorphology and micro-CT scanning methods to detect fragments of termite mounds in ash-rich sediments within a Holocene archaeological site in Brazil, as evidence of their possible use in earth ovens. A more recent study by Leierer *et al*. (2020) couples micromorphology with lipid biomarker analysis to help identify fuel sources and burning temperatures in a pit fire in a Middle Palaeolithic site in Spain.

In contrast to small, open fires, cooking in an earth oven occurs within a closed, or reducing atmosphere, often with steam as the main cooking agent (Willams 1985, p. 110). Hence deposits associated with earth ovens would tend to have a higher proportion of charcoal than ash. Temperatures reached during the cooking process in earth ovens are likely to be high (>500°C) and should be reflected at macro- and microscale in the surrounding earth (Gur-Arieh *et al*. 2013; Singh *et al*. 1991), as well as by the presence of heat-fractured rock or altered bone (e.g. Shipman *et al*. 1984; Table 1). Martin (2011), for example, used the common presence of fused silica particles and white (rather than grey) calcined bone to indicate heating temperatures of between 600°C and 900°C in one excavated mound oven. More empirical measures of temperature can be gained from use of Fourier Transform Infrared spectroscopy (FTIR and micro-FTIR) techniques (Ellingham *et al*. 2015) but these have yet to be applied more extensively in Australian archaeological contexts (e.g. Lowe *et al*. 2018). Other features of earth ovens include partially-combusted plant matter, as well as greater quantities of larger, solid charcoal (Fig. 1B) as a result of the low oxygen conditions, which may or may not be present (e.g. Martin 2011; Whitau *et al*. 2018).

Figure 1 shows a sequence of (shallow) dug combustion features, including one interpreted as an earth or ground oven, from the ancient site of Riwi in the southern Kimberley (Fig. 1) (Whitau *et al*. 2018; also Vannieuwenhuyse 2016). A sharp boundary and

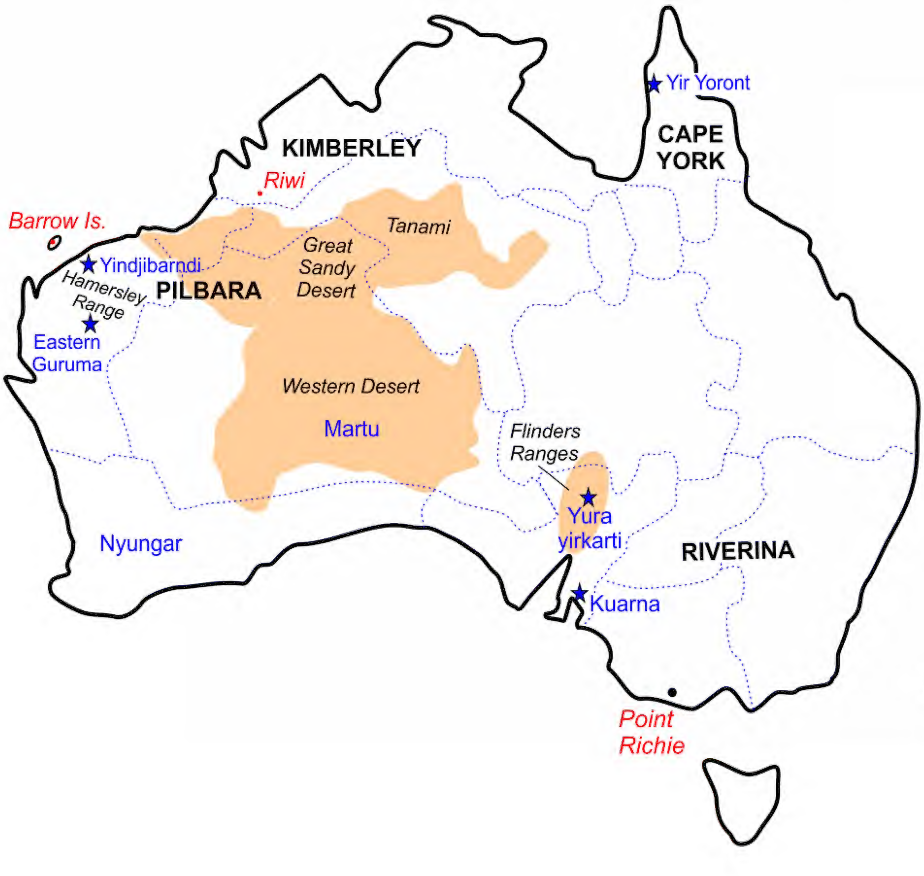

Figure 1. Simplified map showing regions (black text), approximate distribution of major language subgroups (blue dotted lines) and specific language groups (blue) and sites (red) mentioned in text

bedded, orientated particles at the base of the lowermost combustion feature (Fig. 2C) indices possible cutting into an older surface. Geogenic sediment within earth oven structures could be related to the covering of the fire with sediment, or may relate to preservation and whether the combustion feature is buried or not (Mallol *et al*. 2017). Ultimately more ethnographic and micromorphological studies are needed of traditional earth ovens to fully understand the variation and complexities around these.

Shallow pit and surface fires

Whilst they may have many purposes, the assumption—especially where wood has been completely combusted—is that surface fires are mainly expedient fires built for short-duration activities (e.g. Mallol *et al*. 2007; Friesem *et al*. 2017; Whitau *et al*. 2018). Unlike pit-hearths, hearths associated with surface fires are not dug into the substrate but merely sit atop it. They may, however, still entail a prepared surface and may preserve thin stratified lenses of ash and charcoal if left undisturbed and are buried quickly. A typical in situ hearth context shows burnt sediments below and sometimes above a well-defined (wood) ash layer (Mentzer 2014; Friesem *et al*. 2014; e.g. Fig. 3). These burnt sediments are sandwiched between unconsolidated surface sediments and an underlying ironstone unit, both into which burnt material has been mixed (Fig. 3).

Open fires are often used for a source of warmth and light, to warn off animals and as an important hub of social gathering (Douglass 1988; Pyne 1991; Dunbar 2014; Wiessner 2014), and for a variety of activities making use of fire energy (e.g. tool manufacture) and combusted materials (Pyne 1991; Friesem & Lavi 2017). Firelighting may utilise firesticks—*boorna karla/karlmoorl* in Noongar; *tjangi* in Martu; *koch* in Yir-Yiront lexicon— or *boya* stone (Douglass 1996), and may involve the use of grass, dried bark (*likarra*) or dung (*kuna,* Douglass 1988). Whilst it may be possible to distinguish stem, bark and grass or grass phytoliths, or similarly dung or spherulitic remains of dung (e.g. Vannieuwenhuyse 2016) in micromorphological thin section, it may be harder to determine whether these derive from natural or cultural processes.

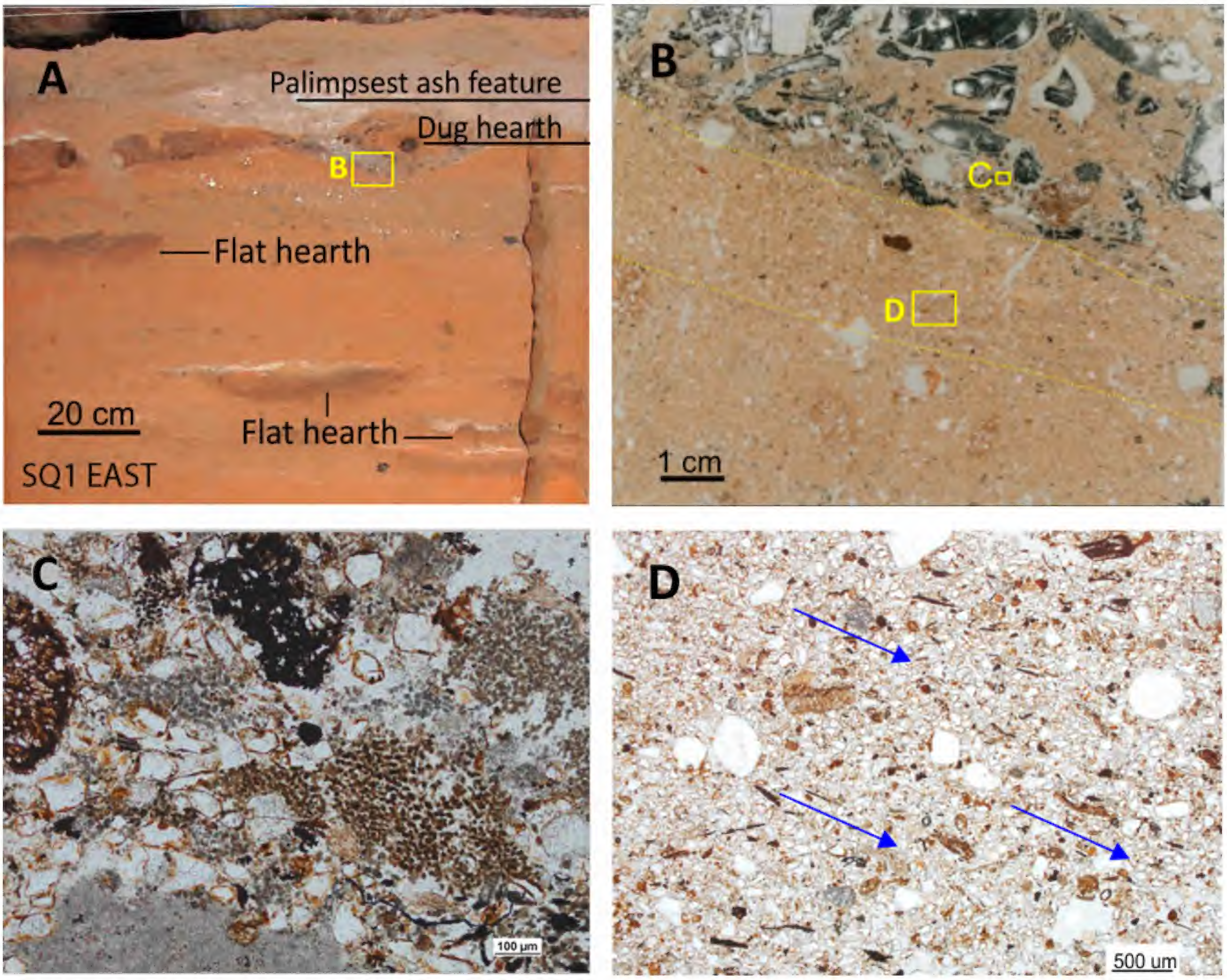

Figure 2. **A**. Field photograph showing a dug combustion feature overlying surface fires (flat hearths) in an excavation profile from Riwi in the Kimberley. **B**. The sharp basal transition of a dug hearth or earth oven within thin section R507 from this profile. Photomicrographs (plane-polarized light) from thin sections show: **C**. mixed charcoal fragments, ashes and geogenic sands, and **D**. bedded, orientated (direction indicated by blue arrows), organic particles below the combustion feature that could indicate digging. (Image modified from Whitau *et al*. 2018, fig. 8; Photomicrographs provided by Dorcas Vannieuwenhuyse).

Cooking (*dookerniny* in Noongar, *kampa* in Yindjibarndi) with surface fires (flat hearths) or dug hearths (pit hearths) may involve direct roasting over hot charcoals (*karl*, e.g. snakes, small mammals, insects), baking in the ashes (*karl-teerdup*, e.g. snakes, frogs, fish, dampers) or use of heat-retainers and hence may be expected to cover a broad range of temperatures. Food (e.g. fish, nuts) was sometimes wrapped in mud or soft bark before being covered in hot ashes (e.g. Meaghar 1975; Dilkes-Hall 2014), the remnants of which may be preserved at the microscale. Meagher (1975) describes the cooking of waterfowl in this way; when the baked mud was cracked open the feathers came away in the mud leaving the body clean. Microscopic evidence of feather barbules—probably from duck—have been found on Australian stone tools (Smith *et al*. 2015; see also Robertson 2002) hence potential exists for micromorphological evidence of bird feathers to also preserve. Again consideration needs to be given to a possible natural origin of faunal remains, such as from degradation of omnivorous coprolites that may contain feathers, tiny bone fragments, hairs, scales and insect fragments (e.g. Ward *et al*. 2019).

Another purpose of surface fires is for steaming or smoking. Smoke (*karl boyi* in Noongar, *yulyurdu* in the Tanami region) and the making of smoke (*kampa-purrkunku* in Yinjibarndi) is important in ceremonial and medicinal practices—to cleanse the spirit, including smoking of babies after childbirth ('baby cooking') [iii], to prevent the spirits of Old People from following a visitor to a place home, or for young boys after initiation (Richmond 1993; Scherjon *et al*. 2015; Musharbash 2018). Smoke is also used for therapeutic inhalation. The leaves of *Eremophila longifolia* (Berrigan emu bush), for example, is particularly favoured for smoking purposes as it produces a smoke with significant antimicrobial effects (Richmond 1993; Sadgrove *et al*. 2016). One variation thereof involves the creation of a bed of thick leaves over very hot stones, on which the patient was laid and then buried in warm sand up to the neck for several hours (Sadgrove & Jones 2016). To create smoke, leaves rather than tree wood is used, and this distinction may be visible from microscopic plant residues.

Figure 3 shows the remains of a surface fire as represented in a stratigraphic section, with baked sediment below (but not above), ash and charcoal deposits. The presence of ash particles in an anatomic connection (Fig. 3A) indicates the fire was in situ, and that such structures were not used repeatedly (Friesem *et al*. 2014; Mentzer 2014; Whitau *et al*. 2018). The hearth and surrounding sediment contain abundant (~20%) carbonised and degraded (but unidentified) plant

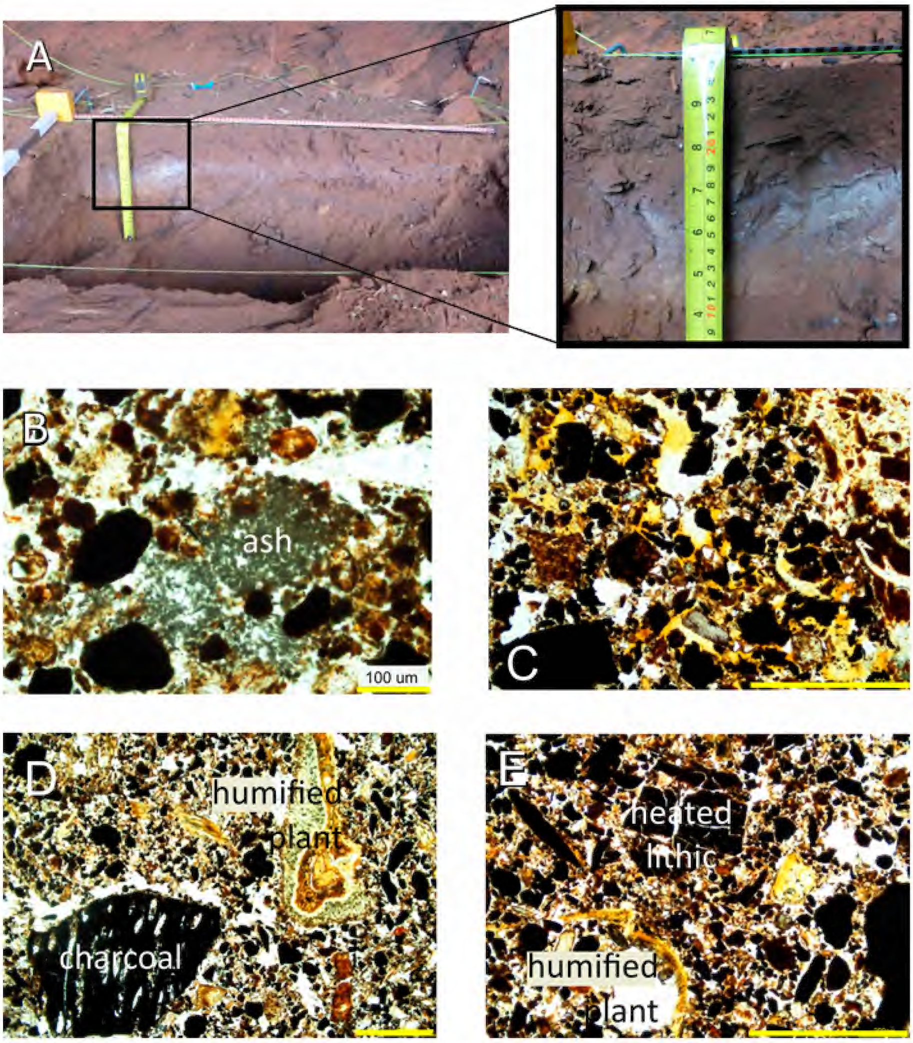

Figure 3. **A**. Field photograph showing a typical in situ hearth from a shallow excavation profile in the eastern Pilbara, with the remains of one or more burning events represented by charcoal and ashes overlying baked sediment. Photomicrographs of thin sections from this profile show: **B**. rhombic ash in anatomic connection and possible resin; **C**. possible resin (yellow stain); **D**. humified plant material and charcoal fragments; and **E**. fire-cracked rock with ferrugenous matrix. All photomicrographs are displayed in plane-polarized light and yellow scale bars are 1 mm unless marked otherwise. (images by IAKW).

[iii] See also Central Australian Aboriginal Media Association Productions (2001) https://www.nfsa.gov.au/collection/curated/smoking-baby-muluru

material, including root, stem and leaf tissue from which resin appears to have been exuded (Fig. 3C). The inferred presence of resin in the deposit may derive from a highly volatile plant (e.g. spinifex) that was used as a firelighter, or the fire may have had a medicinal or other purpose. Although there are some burnt bone fragments, the predominance of plant material and small size of the hearth implies cooking was not its main purpose. Walters (1988) has noted that, in some instances at least, fires of First Nations people are kept clean and bone and

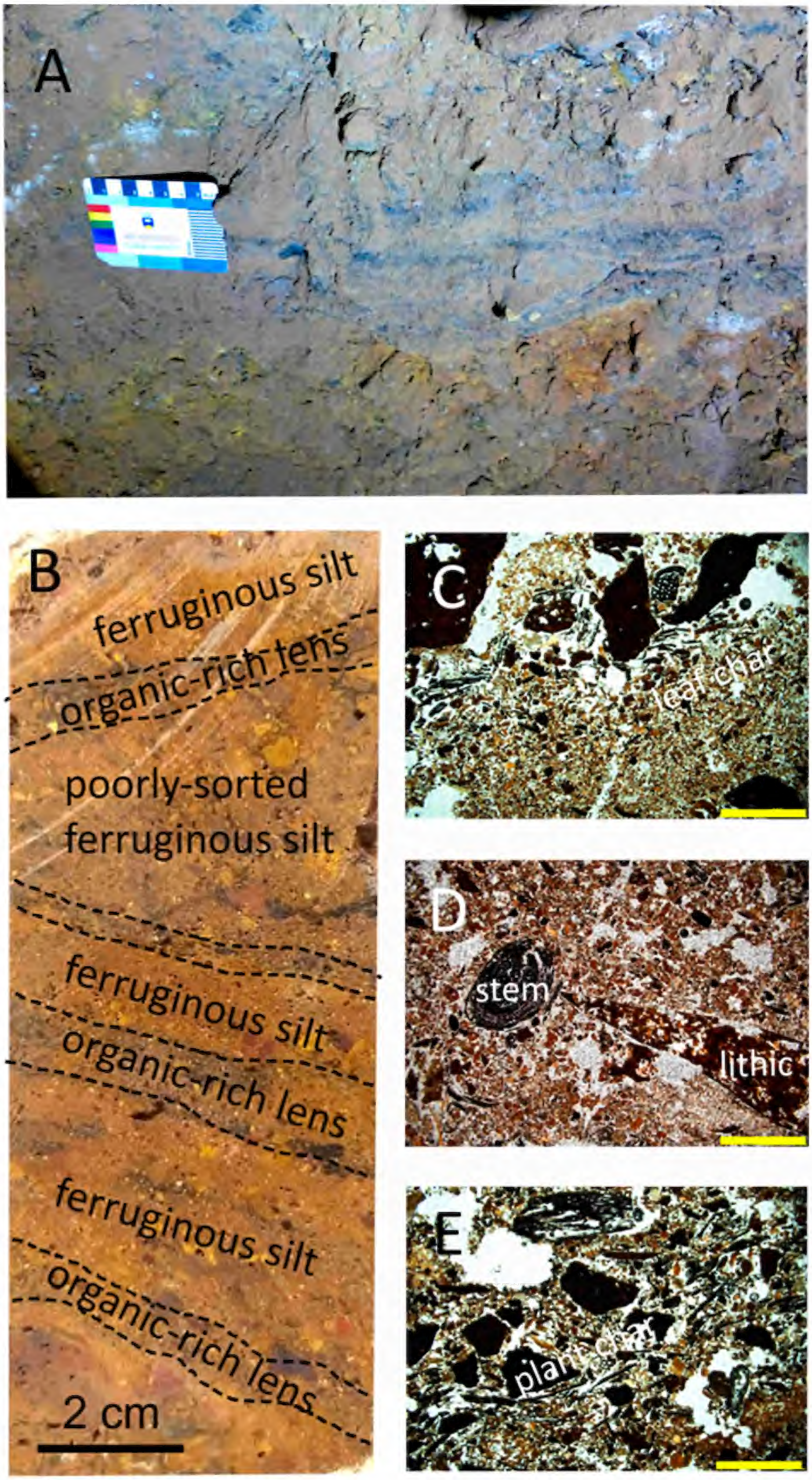

Figure 4. **A**. Field photograph of an excavation profile from another eastern Pilbara rockshelter showing a sequence of charred plant laminae interposed between ferruginous silty sands; **B**. Scan of the resin-impregnated block showing repeated (up to 9) microstratigraphic units. Photomicrographs of thin sections showing: **C**. laminar plant char over fine silt; **D**. lithic fragment (possible artefact) and charred plant stem and **E**. laminar plant charcoal and ash. All photomicrographs are displayed in plane-polarized light and the yellow scale bars are 1 mm (images by IAKW).

Table 1. Typology of combustion features (modified from Homsey & Capo 2006; Mentzer 2014; Goldberg *et al*. 2017; Whitau *et al*. 2017).

Combustion type	Archaeological expression		Taphonomy	Possible function and associated language
	Macro-	Micro-		
Earth/rock oven (ilda[i], kupmurri[ii], mirrnyong[iii], yulh-tha[iv])	• Intrude (prepared) surfaces • Basin profile • Charcoal-stained rocks (rock oven)	• High temp. burning ~500–900°C • Burned earth clasts • Thermally-altered rock • High geogenic content • Burned micro-artefacts (e.g. stone tools) • Partially-combusted organic matter	• Ovens often swept and reused and unless sealed, fire residues may have been removed. • Low post-depositional alteration (unless exposed)	• Cooking/steaming (dookerniny[v]; warukurrkaltj[vi]) • Lithic treatment
Surface hearth	• Prepared surface • Shallow profile (not dug in) • May be rock-lined	• Charcoal-rich or ash-rich (may preserve thin alternating layers of ash and charcoal) • Partially-combusted organic matter • Calcitic cellular pseudomorphs • Broad range of temperatures • (~200–500°C)	• Shallow, hence high post-depositional alteration	• Smoking/fumigation (puyu[vi]) • Quick cooking, e.g. opening shellfish • Light (nyurnmatjali[vi] • Warmth (yakunpa)[vi] • Social hub
Shallow pit hearth (karlup[v], yuwarta[vii])	• Prepared surface • May be rock-lined • Lens-shape profile	• Distinctive layers (from bottom to top) including altered/rubified soil substrate, charred remains and charcoal, ash layer • Articulated ash aggregates • May contain thermally altered rock • Moderate temp. burning ~200–600°C	• Shallow, hence high post-depositional alteration	• Cooking (dookerniny) including roasting, broiling, hot ash (thum-nhaq)[iv] • Light (nyurnmatjalivilorrn[iv]) • Warmth • Social hub
Tree hollow hearth	• Prepared area • Burning mainly internal (minimal external) • May be clay-lined (insulated)	• Charcoal-rich • Low geogenic component • May contain heated clay fragments • May contain evidence of termite activity	• Tree-cavity may be natural (e.g. termite, decay) or cultural (created with use of fire) • Area around tree hollow cleared of leaf litter • Sometimes lined by clay	• Cooking, inc. smoking (karlboy[iv], yulyurdu[vi]) • Social hub • (Shelter)
Maintenance (swept combustion feature)	• Heteregenous units	• Multiple microfacies • Splintered, fragmented charcoal and bone • Burned microartefacts	• Mixing evident from disturbed ash particles	• Discard
Secondary ash dump	• Relatively thick units • Lens/dome like shape	• Mixed deposit • Chaotic microstructure • Charcoal or ash-rich • Partially-burnt material • Low geogenic content • High porosity • Slight orientation of charcoal grains	• May be reworked or bioturbated	• Cleaning by-product

Language key: [i] South Australia (Tunbridge 1985); [ii] eastern and south-eastern Australia (Chauncy 1878), [iii] Torres Strait Islander and some Cape York people (Monaghan 2007); [iv] Yir-Yiront, Cape York (Alpher 1991); [v] South West Australia (Douglass 1996); [vi] Western Desert (Douglass 1988), [vii] Yinjibarndi, Pilbara (Wordick 1982).

rubbish are not discarded into the fires. Yet anecdotal evidence suggests that bone, especially fish bones, may be discarded into fires to avoid accidentally stepping on them (Lynley Wallis pers. comm. 2021). As such, absence of bone *per se* cannot be indicative of purpose.

Another interesting example of a site featuring combustion features rich in plant material is shown in Figure 4. Excavation of this eastern Pilbara rockshelter site revealed a series of relatively thin (< 2 cm) layered black, organic-rich units (approx. 30 cm across) interspersed with otherwise relatively homogenised iron-rich, silty sediment. In thin section some dark units have sharp boundaries, possibly indicative of surface preparation or alternatively a natural erosive event. This sequence shows repeated intact units of burnt, predominantly monocotyledon, plant material and minor ash (Figs 4C–F) that may be due to burning of bedding/floor matting, smoking to repel insects, or some other repeated activity. The stacked nature of the combustion structures imply a long hiatus between firelighting events (Mallol *et al*. 2013). Archaeological deposits generally also contain bedded unburnt vegetal tissue, which may evince human behaviour associated with combustion features (e.g. matting, wrapping for food items) or they may be naturally deposited (e.g. wind-blown leaves; Miller *et al*. 2010; Ismail-Meyer 2017).

Clearly the type of wood used in fire is an important part of identifying purpose, as different wood species will burn hotter and cleaner (e.g. Acacias), create more smoke for medicinal (e.g. *Eremophila, Callitris, Geijera*) or as an insect repellent (e.g. *Santalum* sp.; e.g. Specht 1958; Bindon & Peile 1986; Kamminga 1988; Sadgrove & Jones 2016; Sadgrove *et al*. 2016). These species usually have region-specific names that reflect local knowledge of plant use; a report by Ecoscape (2018) for example, lists Eastern Guruma (eastern Pilbara) names for plants including *wintamarra* for mulga (*Acacia aneura*), *nhirti* for emu bush (*Eremophila cuneifoli*) and *putaty* for sandalwood (*Santalum spicatum*). Some of these listed plants were identified for fire making, including kapok (*Aerva javanica*), kerosene grass (*Aristida contorta*) and camel bush or *kalyartu* (*Trichodesma zeylanicum*).

In Noongar country, resin such as that from the *Xanthorrhoea* (balga grass tree) was used to start fires using a balga stick (*mirliny*). In this region particular rocks, such as white quartz (*bilying*), were also used for firemaking (Douglas 1996), hence identification of rock types as well as plant species may also be relevant to understanding past fire use. Obviously fire studies can benefit from multiple approaches including micromorphology, anthracology (or other plant identification methods e.g. Whitau *et al*. 2018), ethnography and language.

Maintenance and secondary ash dump (rake-out) features

The repeated or multipurpose nature of anthropogenic fire use involves some level of management, including from the extinguishing of the fire (*warrugalgu* in Ngarluma (coastal Pilbara)) to the raking out of hearths, sweeping and dumping of debris elsewhere (O'Connell 1987; Fisher & Strickland 1989; Goldberg 2003; Friesem & Lavi 2017; Friesem *et al*. 2017). The micromorphological expression of a burning palimpsest will vary depending on the original nature(s) and purpose(s) of the fire(s) and the type(s) of maintenance practices (Friesem *et al*. 2017; Mallol *et al*. 2013; Miller *et al*. 2010) as well as any post-depositional trampling or reworking. Similarly, rake-out features and secondary ash dumps will display great variability although the accumulated material is likely to be highly heterogeneous and showing a chaotic structure (i.e., no preferred orientation; Table 1). It has been suggested that some earth mounds began as places to dump cooking refuse (Williams 1985, p. 304). More important is the complete lack of baked substrate that would otherwise indicate in situ burning (Schiegl *et al*. 2003; Friesem *et al*. 2014; cf. Mentzer 2014). The importance of differentiating rake-out features from in situ hearths is to highlight differential use of space in and around archaeological sites (Friesem & Lavi 2017, 2019) and one of major advantages of a micromorphological approach to assessing this is that small objects are more likely to remain in primary context (Meignen *et al*. 2007).

Figure 5 shows an example of a possible rake-out feature from a large coastal cave on Barrow Island, off the Pilbara coast (Fig. 1). An excavation against one of the walls near the front entrance exposed a 50 cm-deep highly mixed deposit (Fig. 5B) with significant post-depositional alteration. Micromorphological analysis of the deposits revealed a mix of charcoal (Fig. 5B), burnt and unburnt teeth and bone (Fig. 5D), shell (Fig. 5E), patches of ash (Fig. 5F) and fine silts. Whereas these secondary deposits were not particularly notable in themselves beyond the variety of debris they contained, they were of interest because they provided the best association for any kind of combustion feature, which has yet to be unearthed at the site. This rake-out deposit is close to the entrance and within the immediate area of occupation rather than farther back in the cave (cf. Schiegl *et al*. 2003). This likely increased the reworking of the deposit by burrowing fauna or by humans moving in and out of the cave, although there was no obvious trampled material observed in the thin section.

Other hearth types

To date there do not seem to have been any micromorphological studies of shell middens or shell midden hearths in Australia, although there is growing literature on this elsewhere (e.g. Aldeias *et al*. 2019; Villagran 2019). The term 'midden' is of Middle English derivation (from early Scandinavian; Danish: møding, Swedish regional: mödding) according to the *Oxford English Dictionary* (3rd edition, 2003) and there may have been a comparable word or phrase used by First Nations people for a midden-hearth. There have been many studies in Australia relating to cooking shellfish, most notably that of Meehan (1982) that may aid future micromorphological studies. The shellfish cooking fires described by Meehan (1982) were mostly surface fires and less commonly using an 'oven' made of old shells and charcoal. The fire-related traces created by cooking shellfish range from thin to very 'ample' deposits of ash and charcoal, the latter sometimes accompanied by shells that had been used as 'heating plates' (Parkinton *et al*. 2009, p. 110).

Another poorly documented type of combustion feature are tree hollow hearths (Pyne 1991; Builth 2014),

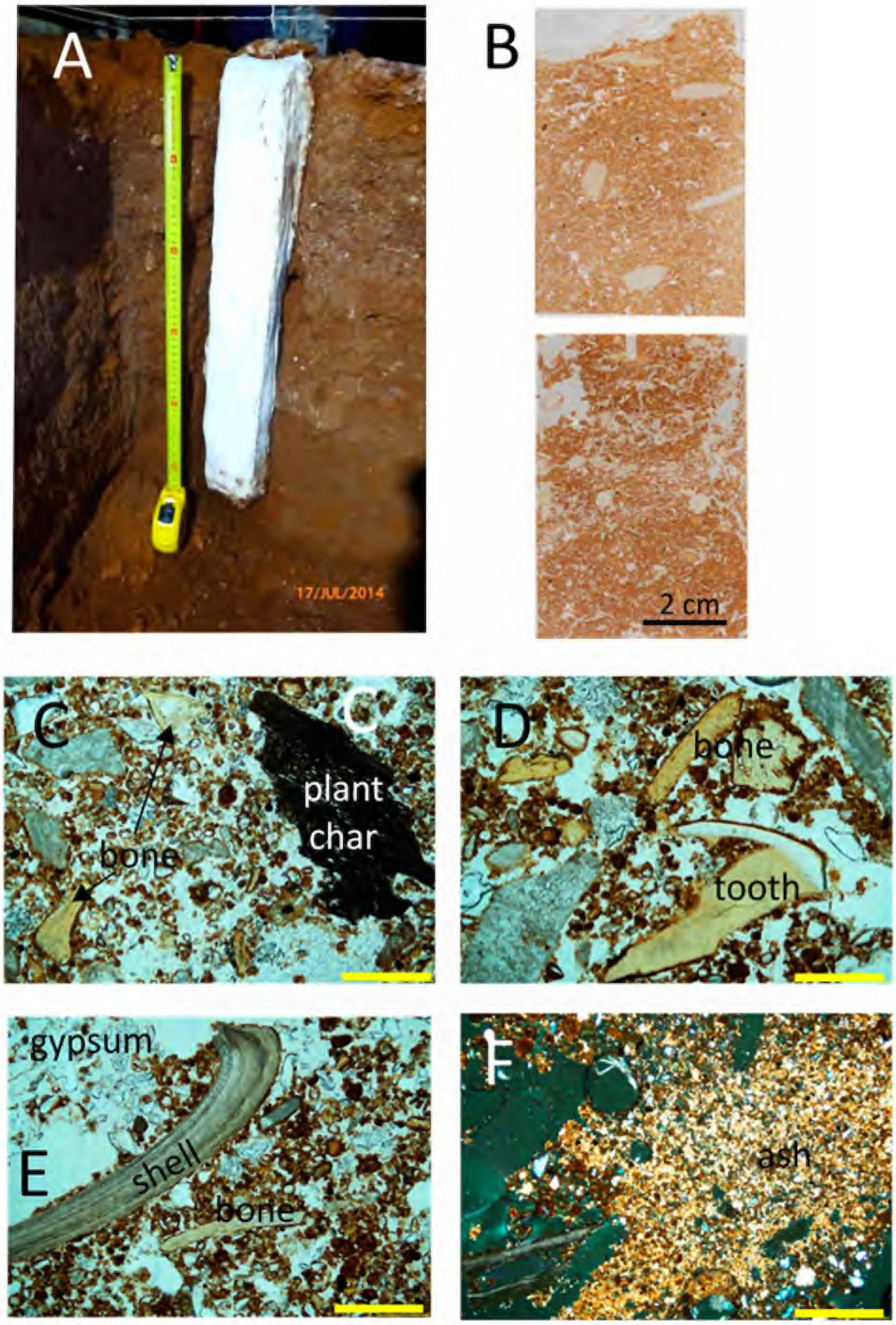

Figure 5. **A**. Field photograph showing resin profile sampling of a probable dump site, positioned against a rockshelter wall in a coastal cave on Barrow Island; **B**. Thin sections showing a largely homogenous sediment profile. Photomicrographs (plane-polarized light, unless otherwise stated) from thin sections within this profile show: **C**. plant/charcoal and bone (b) fragments in a matrix of limestone and fine clay; **D**. tooth and bone (b) fragments; **E**. shell and bone (b) fragments with gypsum (g) in voids; and **F**. concentrated area of micritic ash (cross-polarized light). Yellow scale bars are 1 cm. (images by IAKW).

which use natural hollows at the bases of trees or fallen trunks as ovens, smoking chambers or fire depots. Such features are more common on landforms that could otherwise not be dug into and/or where climatic conditions made it very difficult to find any shelter to cook staple foods—and where such landscapes had large trees. Larger hollows could even be used for shelter (Pyne 1991), and thus might have hearths built within them. Evidence in support of cultural burning within natural tree hollows tends to manifest as burning on only one side of the tree rather than around the whole circumference as in a natural bush fire. Clay may also have been used to line the interior hollow of the tree, thereby insulating them (Pyne 1991, p. 90). Although not documented, the use of hollowed trees as a protected space for smoking, fires or shelter may also extend to the wet south-west region of Western Australia where karri forests are endemic (Heather Builth pers. comm. 2021). Separated from the immediate substrate, such hearths might be expected to contain less geogenic sediment and more charcoal, with micromorphological evidence of bone or food residues and heated clay if used.

An example of an unusual hearth is a Kuarna 'burial hearth' documented by Owen & Pate (2014) in which 'hearths' (not described) were positioned over the hands of an individual as if to 'bind' them to the grave. A series of hearths (again not described) extending beyond the burial were interpreted as part of a 'sorry camp' connected with burial customs and the mourning period.

Further insight on these hearth types might be gained from micromorphological analysis and from the language used to describe them.

NATURAL VERSUS CULTURAL COMBUSTION FEATURES

Fire is a common element of the Australian environment even without humans, and natural fire events can result in deposits with similar characteristics to those formed through anthropogenic burning. An example of the importance of identifying anthropogenic hearth fire is particularly apparent at Moyjil (Point Ritchie) in Victoria, which McNiven *et al*. (2018) controversially postulated to date to the Last Interglacial. McNiven *et al*. (2018) identified the hearth as a concentrated area of charcoal and darkened sediment, and what appeared to be burnt sediments and rocks. Discriminating criteria were used to distinguish this as a cultural hearth from a naturally burnt feature (McNiven *et al*. 2018, table 3) but micromorphological analysis is still pending. Potential also exists to explore differences in residues from bushfire and hearth fires using microanalytical techniques, including signatures of heating on soil, wood charcoal and bone of native fauna (Berna *et al*. 2007; Weiner 2012; Ellingham *et al*. 2015). In general, the presence of rubified sediment or fire-cracked rock, charcoal or articulated ash lenses can all be used to identify intact combustion structures or hearths but none are unequivocal indictors. The presence of cultural material such as bone fragments of economic fauna, multiple charcoal taxa, ochre or exotic stone fragments, would support an interpretation of human activity (Barbetti 1986).

While work towards differentiating cultural and natural fire signatures in the sedimentary record is ongoing and beyond the scope of this study, useful insights may be gained from ethnography and language around cultural burning in order to inform future micromorphological studies. Foremost is that the vocabularies of First Nations people contain many words for fire whereas distinction is made between hearth fires and bushfire (Pyne 1991, p. 91). This is exemplified in semantic networks (e.g. Fig. 6), which show links between words associated with fire, camp and country. Distinction is made between bushfire, grassfire, fire, firewood, firestick, ash, charcoal, etc. with some words showing polysemy and common cognate sets. These cognate sets link languages with their geographic location and genetic affiliations, so that words can be used to generate maps relating not only to given meaning pairs but also human-behavioural processes relating to fire and country.

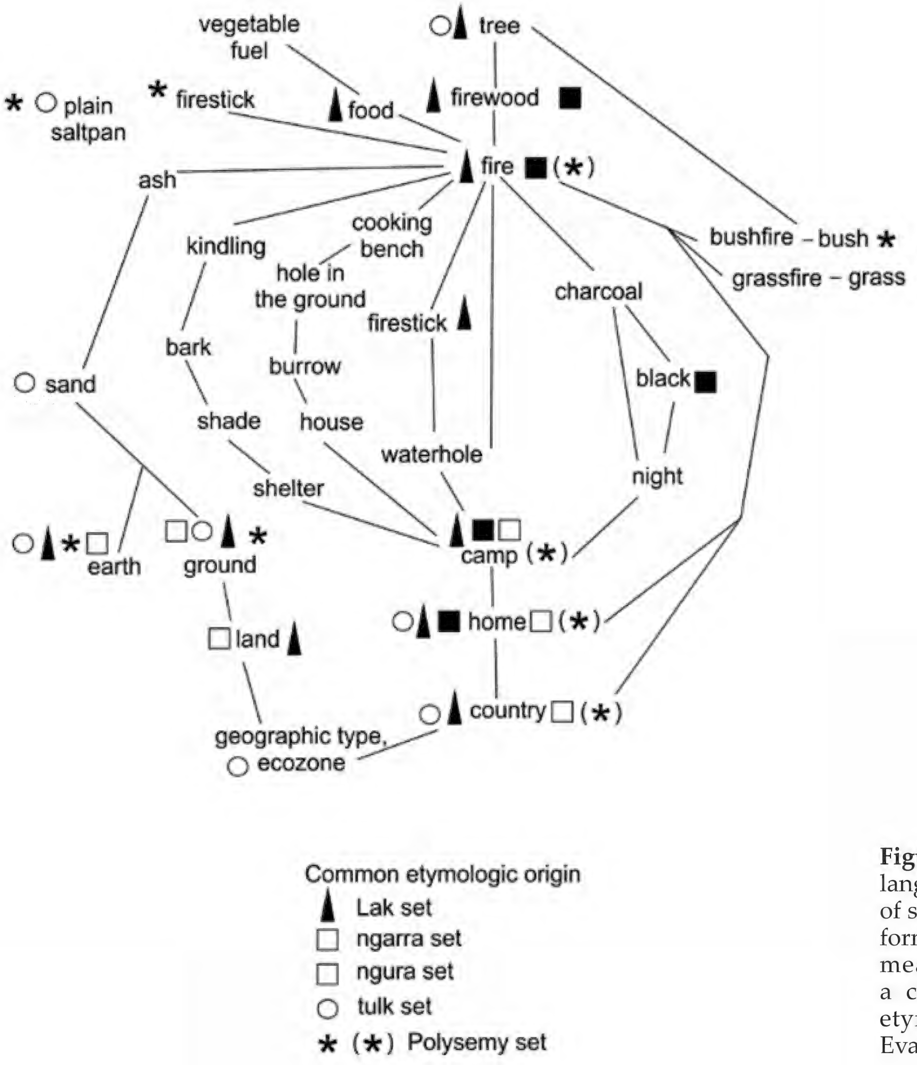

Figure 6. Part of the fire/camp/country language nexus representing networks of semantic connections. Lines indicate formal paths or connections between meanings, which themselves have a common linguistic derivation or etymological origin (modified from Evans 1992).

The pre-European fire regime in Australia is generally regarded as comprising frequent, low-intensity fires designed to increase the availability of resources (Gammage 2014) but, as Kelly (1998) explained for southern Western Australia (Noongar country), both frequent cool fires and less frequent, high-intensity fires are needed to manage the country. Cool fires (*karla nyidiny*) in early summer (*birak*) are aimed at promoting new growth, while still a little moist to force out animals (*barna*) and provide easier access through the bush (*marlark*) or country. Hot fires (*karla karlang*) are needed every decade or so, to maintain thick growth in some areas. The latter, however, are different to natural forest fires that sometimes result from build-up of undergrowth and have greater impact on soil organic matter and heating (Talua 2015). Kelly (1998, p. 12) also indicated that there are many other fire types, including those used for driving game, protection of upper canopy species, and making particular root crops more palatable (see also Scherjon *et al*. 2015).

Martu people of Australia's Western Desert, for example, have a rich language around fire that link people in their various life stages to landscape at different stages in the fire cycle, and the various methods for burning when hunting particular animals. *Nyurma* describes newly burnt ground, and *waru-waru* describes land where shoots have started to sprout; *mukura* (*nyukara*) occurs after a few years when edible plants are fruiting and seeding, and later still *mangul* commences when the growing spinifex starts to outcompete edible plants, leading to *kunarka* when the advanced spinifex starts to die and leaves behind sterile hollows (Bird *et al*. 2008; also https://www.kj.org.au/news/the-language-of-waru-fire). In short, fire is a word that encompasses an enormous variety of human activity with a wide diversity of cultural meanings and archaeological presentation, which is only just beginning to be explored.

CONCLUSIONS

Language is shaped by our need to communicate precisely and efficiently (Regier *et al*. 2016). The importance of fire for First Nations people has produced a wide vocabulary of associated words. It follows that an understanding of how First Nations Australians used, controlled, related to and thought about fire is a key part of interpreting combustion features in the Australian archaeological record (and may have important ramifications for interpreting similar features of gatherer−hunter−fisher communities elsewhere). One way to achieve this is through the combination of traditional knowledge and archaeological science, including micromorphology.

As Mentzer (2014) noted, micromorphology is not a panacea for making the identification and interpretation of fire in the archaeological record easy or simple. Nevertheless, it can reveal greater complexity in a site or sites, just as language associated with the word fire can also be demonstrative of great complexity. Such complexity is critical in providing a better understanding of the depositional and post-depositional history of combustion features and burned remains, and a more nuanced understanding of hearths as a cultural hub for past occupants throughout Australia. Whilst our review is not comprehensive, it does try to demonstrate that darkened charcoal or ash-rich features in archaeological excavations are as complex and nuanced as the language around fire and are worthy of greater attention and differentation.

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Journal of the Royal Society of Western Australia, 104: 25–26, 2021

Alexander William Robert Bevan

BSc, PhD (U Lond)

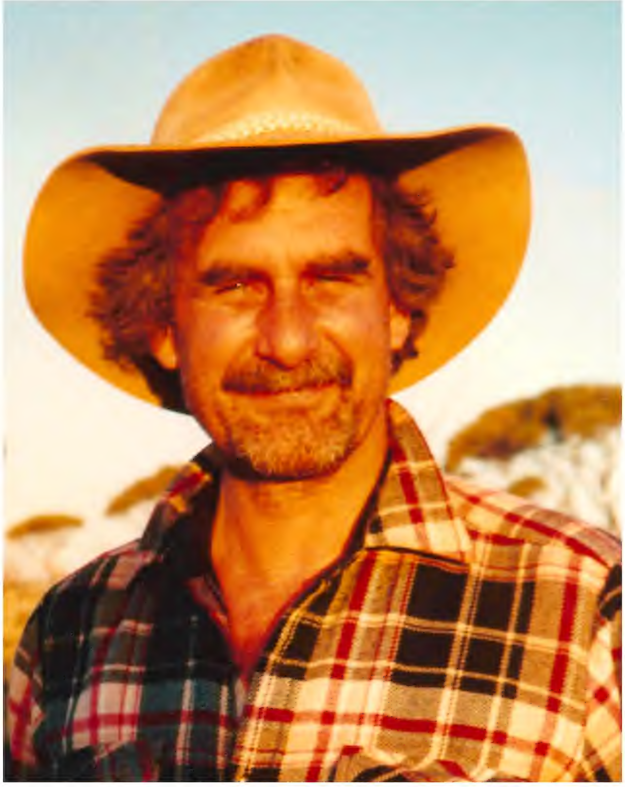
25th July 1951 – 11th February 2021

The recognition that meteorites accumulate in desert regions, and that co-ordinated searches could significantly increase the number of samples available to researchers, has revolutionised the field of meteoritics. The availability of tens of thousands of desert meteorites is now taken for granted. This year saw the loss of one of the figures who saw that potential and organized multiple expeditions in the Nullarbor Plain of Australia to make such collections a reality. Alex Bevan died aged 69 on 11th February 2021.

Alex was born on 25th July 1951, in Bridgend, Glamorgan, in Wales to parents Ceinwen and Colin Bevan. They lived in St Brides Major, a small village close to the central south coast of Wales. He was an only child who grew up roaming the Welsh countryside, including fossil-studded limestone cliffs and quarries, which triggered his interest in geology.

In 1969 he read Geology at University College London, obtaining his Honours degree in 1972. He first worked in the library of the Geological Society of London in Burlington House on Piccadilly, then took up a position in 1973 as Assistant Scientific Officer in the Meteorite Section of what is now the Natural History Museum in South Kensington. After some years there, and promotion, he began a part-time PhD on the metallurgy of meteorites as part of a joint University of London/Government Laboratories scheme. The work involved research at Manchester University under Howard Axon at the Institute of Science and Technology and at Lehigh University in Pennsylvania in the USA. He obtained his PhD in 1985. It was at the Natural History Museum that he met Jenny Leverton, a close colleague in the Department of Mineralogy. They married in 1974 and continued to work together, publishing several joint papers.

In 1984, Alex came to Perth to appraise and assist with the meteorite collection at the Western Australian Museum. While he was in Perth a meteorite fell within sight and sound of the city—Alex actually heard the sonic boom. The meteorite was seen to fragment, with one piece recovered from the beach at Binningup where it had landed close to two women sunbathing. Alex helped co-ordinate the search for other fragments, and was interviewed for television, radio and the press. Fortuitously, after many years of effort, the museum was in the throes of trying to appoint a Curator of Minerals and Meteorites. All that was needed was for final approval for the position to be given by higher echelons of government. The Binningup meteorite's spectacular entry into the state provided that impetus, so approval was duly given the week after its arrival—truly 'Manna from Heaven'. Head of Department, Ken McNamara, strongly advised Alex to apply for the position and the rest, as they say, was history. Alex, Jenny, and their young children Sarah and Tom arrived in Perth in September 1985.



Alex quickly realised that the Nullarbor Plain in Western Australia might be a productive source of meteorites. A local bushman, John Carlisle, had found several meteorites there while out rabbiting, including the 11 tonne Mundrabilla iron. Soon after arriving in Perth Alex started a program of regular expeditions to the Nullarbor, which from the beginning had an international component. Taking the Antarctic Search for Meteorites program as his model, colleagues came together from all over the world to participate, camping and searching in the Nullarbor Plain for two to three weeks. The results were spectacular. By 1991, Alex's Western Australian Meteorite Recovery program had recovered around 500 meteoritic samples.

With the eye of a metallurgist, Alex would make fundamental contributions to our understanding of iron meteorites over the course of his career as well as continuing his research on meteorites in general. In addition, his success in recovering desert meteorites led to an interest in how they are affected by the terrestrial environment and what this can tell us about their age and history. That interest developed into collaborations

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that would last decades: from meteorite weathering, to constraining impact rate using desert populations, and in the end to the concept of a Desert Fireball Network to track meteorites as they come through the atmosphere and pinpoint fall sites in areas well suited for their recovery. The Desert Fireball Network project became the seed for a growing planetary science group at Curtin University in Perth, which now has 50 staff and student scientists—the largest group of its kind in the Southern Hemisphere. It is a key part of Alex's legacy.

Although meteorites were important to him, Alex also actively worked on and administered the Western Australian Museum's large mineral and rock collections, and for many years was the Head of Earth and Planetary Sciences. He was involved in the organisation of a number of scientific conferences (including the first Meteoritical Society Conference to be held outside the USA or Europe, in 1990) and was an active contributor to several other societies and groups, particularly the Royal Society of Western Australia of which he was President from 2004–2006.

A significant aspect of his work was in public education, for which Alex made regular appearances on TV and radio, and wrote several books popularising the field. He carried out lecture programmes in Perth, regionally and overseas, and was a main instigator of the 'Diamonds to Dinosaurs' gallery at the Museum, which took visitors on a journey from the formation of the Solar System to the footprints of the first hominins. More recently, his contribution to displays in the new Museum in Perth, in the words of the Director, 'stands as a tribute to his work and his commitment to engaging the wider public'.

In January 2018 Alex retired from the Museum after 32 years and five months, but continued to pursue his scientific research, and to teach and mentor undergraduate and PhD students, and post-doctoral researchers, sharing his enthusiasm and knowledge, even whilst undergoing palliative chemotherapy.

After retiring Alex rediscovered a talent as an artist—his favoured media being watercolours and oil pastels. Many friends and family now treasure the paintings he gave them. Alex is survived by his children Sarah, Tom and Matthew, his wife Jenny, and grandchildren Lincoln and Harlie.

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The rare and threatened Western Dwarf Galaxias (mud minnow) near Ellen Brook, southwestern Australia

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The Western Dwarf Galaxias *Galaxiella munda* is a native freshwater fish found only in southwestern Australia between the Vasse and Angove River systems, and in two outlying locations over 300 km farther north near Gingin. An additional two specimens collected from near Ellen Brook in 1973 are held by the Western Australian Museum; however, this record lacks detailed spatial resolution and has rarely been acknowledged in the literature. If from an extant population this would represent an important local range extension of this threatened species. A lack of available data on the freshwater fauna from this area means that further surveys are warranted to assess if the two specimens represent an overlooked extant outlier population. If confirmed, the presence of the species would have considerable implications for its conservation and the protection of local streams and wetlands.

Keywords: *Galaxiella munda*, freshwater fish, threatened fauna, outlier population

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INTRODUCTION

The Western Dwarf Galaxias *Galaxiella munda* (commonly referred to as 'mud minnow'; (Fig. 1) is a diminutive member of the Galaxiidae family and one of six endemic species of freshwater fish from the Gingin–Bullsbrook region, 50 km north of Perth (Morgan *et al*. 1998; Smith *et al*. 2002; McLure & Horwitz 2009; Beatty *et al.* 2010; Hourston *et al*. 2014). Within this region urban development is relatively scant, thus local waterbodies are better suited to maintaining populations of native fishes compared to most other parts of the Swan Coastal Plain. Much of the region is covered by pristine banksia woodland, though there are also sizeable expanses of cleared agricultural lots. The wetlands in this area consist of seasonal damplands, lakes, swamps and brooks (Beatty *et al.* 2010). Most waterways are subject to seasonal desiccation although a few that receive groundwater discharge are perennial (Smith *et al*. 2002; Beatty *et al.* 2010; Hourston *et al.* 2014).

The Gingin–Bullsbrook region hosts outlying populations of two freshwater fish species of conservation significance: *G. munda* is listed as Vulnerable under State legislation (Biodiversity Conservation Act 2016 Western Australia) and the International Union for Conservation of Nature (IUCN; Beatty & Morgan 2019), whereas the Black-stripe minnow *Galaxiella nigrostriata* is listed as Endangered under both State and Federal legislation (Environmental Protection and Biodiversity Conservation Act 1999), and the IUCN (Morgan & Beatty 2019a). In addition, the rare Balston's Pygmy Perch *Nannatherina balstoni*, listed as Vulnerable under both State and Federal legislation, and Endangered by the IUCN (Morgan & Beatty 2019b), was also present in the region until relatively recently, but has not been detected there since 1981 (Morgan *et al.* 1998, 2014). Its disappearance demonstrates the higher risk of extinction faced by these outlying freshwater fish populations compared to their southern counterparts that occupy relatively pristine habitats. Numerous anthropomorphic stressors including secondary salinization, groundwater abstraction, introductions of feral species, climate change, the construction of instream barriers to migration, wetland drainage, and habitat degradation have been implicated in the declines of these threatened species as well as other freshwater fish populations throughout southwestern Australia (Davis & Froend 1999; Hourston *et al.* 2014; Allen *et al.* 2017).

ECOLOGY AND NATURAL HISTORY

Galaxiella munda is typically found in cool, shallow waterbodies, such as brooks, swamps, roadside pools and waterpoints (Morgan *et al.* 1998; Allen *et al.* 2002). These waters typically contain tannins, which tint the water dark brownish red and inhibit visibility. The species also inhabit seasonal waterbodies but perish unless heavy rainfall facilitates access to permanent waterbodies (Pusey & Edward 1990). *Galaxiella munda* prefers acidic water with a pH of 3.0 – 6.5 (Morgan *et al.* 1998), and a low mineral content (Trneny 2001), and struggle to survive in hard, alkaline water with any salt (Morgan *et al.* 2003).

Spawning takes place from July to October, peaking between late August and early September (Pen *et al.* 1991; Morgan *et al.* 1998). The species is a multiple spawner, depositing clutches of eggs within flooded riparian vegetation, similar to other *Galaxiella* species (Pen *et al.* 1991, 1993; Morgan *et al.* 1998). It has a short lifespan, reaching sexual maturity and spawning within the first year of life, before dying a few months later (Pen *et al.* 1991; Morgan *et al.* 1998). The suggestion that

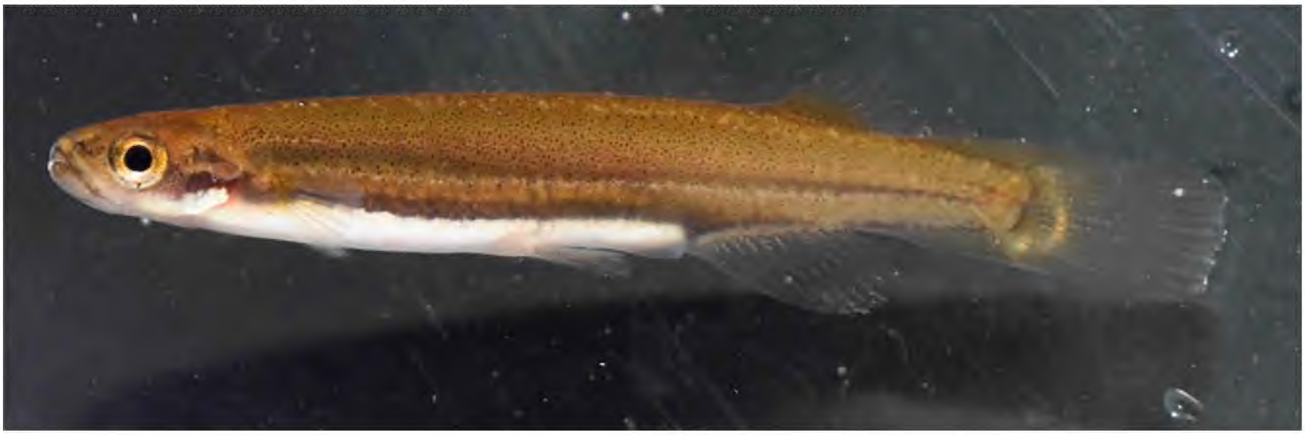

Figure 1. *Galaxiella munda* from the Deep River catchment about 25 km northwest of Walpole; approximately 35 mm long.

larger individuals have a longer lifespan has not been confirmed (Beatty & Morgan 2004). The brief life cycle of both southwestern endemic *Galaxiella* species (Pen *et al*. 1991, 1993; Smith *et al*. 2002) predisposes populations to rapid declines when environmental conditions are unfavourable (Allen *et al*. 2015).

DISTRIBUTION

Galaxiella munda is predominantly found in the southwestern corner of Western Australia from the upper reaches of the Vasse River, near Margaret River, eastwards to the Angove River, near Two Peoples Bay on the south coast (Morgan *et al.* 1998; Morgan & Beatty 2004), with outlier populations near Gingin, over 260 km to the north (Morgan *et al.* 1998; Beatty & Morgan 2004; Hourston *et al.* 2014; Fig. 2). Within the Southwest the species varies in abundance from scarce in catchments such as the Donnelly River (Morgan & Beatty 2006), to seasonally abundant in others, such as the Shannon and Angove rivers (Morgan *et al.* 1998; Trneny 2001; Julian Ackley pers. comm., 2017).

The two outlier populations near Gingin are in Lennard Brook, a tributary of Ellen Brook in the Swan–Avon system, south of Gingin (Beatty *et al.* 2010; Unmack *et al.* 2012; Galvin & Storer 2012a), and in Gingin Brook, a tributary of the Moore River, north of Gingin (Beatty & Morgan 2004; Galvin & Storer 2012b; Fig. 2). Prior to the introduction of feral species, the construction of instream barriers, and clearing of riparian vegetation, both populations are likely to have been more abundant and widespread throughout their respective tributaries. Both tributaries receive groundwater discharge, a common trait of waterways that contain the species and a critical determinant in preserving populations of obligate freshwater fishes, especially within salinized catchments (Morgan *et al.* 2003; Morgan & Beatty 2005; Beatty *et al.* 2011). Although the species was likely historically more widespread, these northern outliers are now the only populations that remain on the Swan Coastal Plain; this drastic reduction in range has been theorised to be the case in *G. nigrostriata*'s outlying populations in Lake Chandala, Melaleuca Park south of Bullsbrook, Kemerton and Gelorup near Bunbury, and *N. balstoni*'s now-extinct Moore River population (Morgan *et al*. 1998; Smith *et al*. 2002; Galeotti 2013; Morgan *et al.* 2014; Hourston *et al*. 2014; Wetland Research and Management 2019a, b).

SPECIMENS OF INTEREST

Two *G. munda* specimens in the collections of the Western Australia Museum, collected in 1973 (Western Australian Museum 2021, unpublished data), represent a potentially significant range extension of the species; however, these records have rarely been mentioned in the scientific literature. These specimens were collected five years prior to the species' formal description and were initially identified as *G. nigrostriata* by McKay (Glenn Moore, Western Australian Museum, pers. comm., January 2021). Subsequent re-examinations by McDowall (1978) and other ichthyologists assigned both specimens (WAM P.22548.001 and P.22549.001) to *G. munda* (Glenn Moore, Western Australian Museum, pers. comm., January 2021).

The specimens were collected during an excavation of a springline near Ellen Brook (How 1978; McDowall 1978; Glenn Moore, Western Australian Museum, pers. comm., January 2021), for which the coordinates supplied are 31°30'S 115°55'E (Fig. 2). No records of this excavation were found by the author although *G. munda* specimens were captured from a nearby artificial wetland adjacent to Lake Chandala in 2001 (Mike Bamford, Bamford Consulting Ecologists, pers. comm., February 2021). Curiously, these specimens were found in sympatry with the introduced Eastern Gambusia *Gambusia holbrooki*, a species whose pugnacious and aggressive disposition typically compromises the survival of small-bodied native fish species, such as *G. munda* (Griffiths 1972; Morgan *et al.* 2004; Beatty & Morgan 2013; Allen *et al.* 2015). It is possible that the WAM specimens and 2001 records are representatives of the same population.

DISCUSSION

Although the author has recorded considerable numbers of *G. munda* within the upper reaches of Gingin Brook (pers. obs. 2020), recent survey efforts by other authors have failed to locate the species in either Lennard or

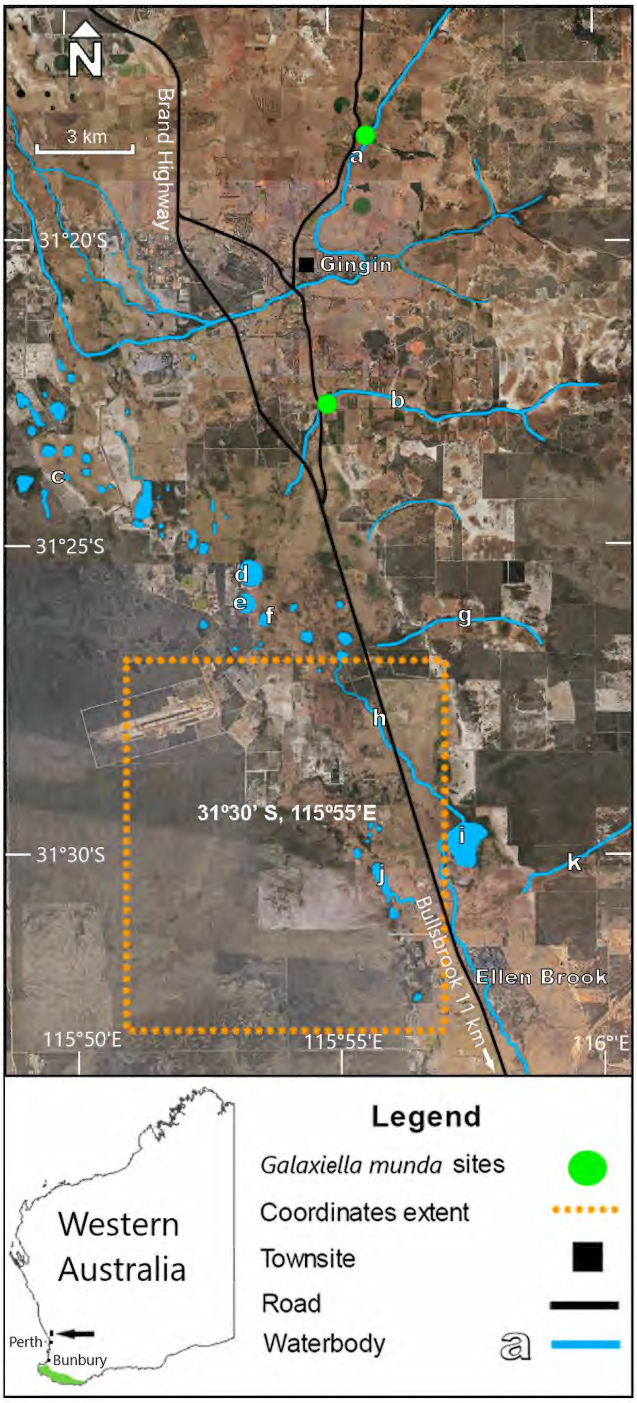

Figure 2. Gingin–Bullsbrook region showing sites with *Galaxiella munda* and various small waterbodies: a) Gingin Brook; b) Lennard Brook; c) Deepwater Lagoon; d) Lake Bambun; e) Lake Nambung; f) Lake Mungala; g) Breera Brook; h) Chandala Brook; i) Lake Chandala; j) Lake Catambro; and k) Yalyal Brook. The study area is arrowed on the inset map, which also shows the main distribution of the species in green.

Gingin Brooks, suggesting there may have been local declines in both tributaries (Galvin & Storer 2012a, b; Department of Water, unpublished data). The introduced *G. holbrooki* has recently been recorded in both tributaries; however, it is not present in the upper reaches of Gingin Brook that *G. munda* inhabits, suggesting an instream barrier prevents the upstream passage of *G. holbrooki* (Beatty & Morgan 2004; Galvin & Storer 2012b; pers. obs., 2020). By comparison, *G. holbrooki* has been recorded at both upstream and downstream sites along Lennard Brook (Galvin & Storer 2012a), likely having an adverse impact on *G. munda* in this tributary.

Further surveys are required to evaluate and record the assemblages of native fishes in the Gingin–Bullsbrook region, as many of the waterbodies in the area remain poorly studied. Specific attention should be given to the poorly studied wetlands in the southern part of the study area, to establish whether or not it has an extant population, as suggested by the 1973 WAM specimens and 2001 records. The only waterbody in the area that has been surveyed for fishes is Lake Chandala; however, these studies have yielded differing findings: Beatty *et al.* (2010) recorded only *G. holbrooki*, whereas McLure & Horwitz (2010) recorded the Nightfish *Bostockia porosa* and *G. nigrostriata*, and Bamford (unpublished data) recorded the Western Galaxias *Galaxias occidentalis*, *G. munda*, Bluespot Goby *Pseudogobius olorum*, the introduced Goldfish *C. auratus* and *G. holbrooki*. Although the waterways in the region show little resemblance to those with *G. munda* elsewhere, comprehensive surveys are required to fully evaluate this possibility. Parallels may be drawn with the recent discovery of *G. nigrostriata* populations at Gelorup, south of Bunbury (Wetland Research and Management 2019a, b), in wetland habitats within cleared agricultural lands that were previously believed to be unsuitable for the species (Morgan *et al.* 1998; Galeotti *et al.* 2010).

Due to the geographical separation between the outlier and main populations of *G. munda*, a great degree of genetic divergence exists (Unmack *et al.* 2012); even populations within neighbouring tributaries of the same catchment can display such divergence (Phillips *et al.* 2007; Beatty *et al.* 2010). In order to preserve these genetically unique populations, captive breeding should be considered, similar to what has been accomplished by aquarium hobbyists for the species' eastern Australian relative, the Eastern Dwarf Galaxias *Galaxiella pusilla* (Leggett & Merrick 1987). It may also be advisable to evaluate if *G. munda* individuals can be translocated from Gingin or Lennard Brooks into an adjacent tributary or wetland deemed suitable for the species. Nearby Yalyal Brook, southeast of Lake Chandala, may be a viable option (Beatty *et al.* 2010), as may be Breera Brook (Fig. 2).

Various threats such as secondary salinization, introduced species, wetland drainage and degradation, groundwater abstraction, and climate change currently jeopardise the survival of native freshwater fishes throughout southwestern Australia (Allen *et al.* 2017). These anthropogenic threats are most evident within the heavily urbanised wetlands of the Swan Coastal Plain, where native species are extremely scarce in comparison to introduced species (Davis & Froend 1999; Hourston *et al.* 2014). As most of these threats (e.g. feral species invasions, a drying climate) are extremely difficult to manage or mitigate, it is critical that conservation efforts are directed towards remnant populations of native freshwater species, with priority given to the most threatened and restricted species. *Galaxiella munda* is arguably one of the most susceptible to anthropogenic stressors due to its short life-cycle and requirement for near pristine habitat conditions (Beatty *et al.* 2010), as shown by the loss of the species at Big Brook Dam in the Warren River catchment, where it was previously abundant prior to the introduction of the Redfin Perch *Perca fluviatilis* (Pen *et al.* 1991; Morgan *et al.* 2002). The survival of this species within the Gingin–Bullsbrook region is a crucial priority and is contingent on habitat protection and restoration. Captive breeding and translocations should also be investigated as such interventions may be required to conserve these populations in the face of many threats, while further surveys are needed in the understudied waterbodies of the region.

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T. W. Fowler's measurements of sea temperature and density from merchant ships off southern Australia in 1896

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ABSTRACT

In 1896 T. W. Fowler initiated a program of twice-daily measurements of sea-surface temperature and density from merchant ships in Australasian waters. Fowler's temperatures and derived salinities south of Australia along ~35°S reveal now familiar oceanographic features: the Leeuwin Current; high-salinity waters in St. Vincent Gulf; and cold, low-salinity waters of the Southern Ocean. Fowler noted that the temperatures and densities along the ships' passages decreased during 1896, and that they continued to do so over the next three years. This appears to have been associated with one of the largest El Niños of the past 150 years that weakened the Leeuwin Current and allowed the Subtropical Front to move closer to southern Western Australia.

Keywords: T. W. Fowler, Leeuwin Current, Subtropical Front, Upwelling, Oceanography, El Niño

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INTRODUCTION

Little is known of the properties of Australia's oceans prior to the end of World War II. Thus earlier information has considerable value in reconstructing ocean conditions. In 1896, while working as a demonstrator in Engineering at the University of Melbourne, Thomas Walker Fowler (O'Neil 1981) allocated some of his spare time to initiate and run a program in which crew members on 'intercolonial steamships' plying the waters around Australia and New Zealand took seawater temperatures and samples twice daily (Fowler 1898). His work was inspired by the achievements of the 1872–76 *Challenger* expedition and he followed the method of Buchanan of that expedition in measuring densities of the seawater samples using hydrometers.

Fowler (1898) presented tables of measurements from five regions, broken into sub-tables for different seasons. The regions were Fremantle across the Great Australian Bight to Adelaide and Melbourne; Melbourne to Brisbane; the East Coast of Australia north of Brisbane; Melbourne to Bluff, New Zealand; and return to Sydney via Cook Strait. Two other tables presented his occasional seawater temperature measurements on the Bass Strait coast at Sorrento Back Beach, Victoria from early February 1895 to January 1898, probably while staying at his nearby holiday home. These were accompanied by density measurements from February 1896. Presumably it was here that he tried and tested the procedures to be used at sea and in his laboratory.

Fowler's measurements are valuable because they appear to be the first taken from ships on the Fremantle to Melbourne route over several seasons (Fig. 1), and the first to obtain measurements within the Leeuwin Current and other oceanographic features between Western Australia and Victoria. Note that the ships crossing the Great Australian Bight to and from Cape Leeuwin just south of 35°S in 1896 would have been near the shelf edge, where the Leeuwin Current flows to about 120°E, whereas farther east the shelf edge gradually angles east-northeastward. Fowler (1898) reported that the temperatures and densities south of Australia decreased during 1896, and, in an abstract published in 1901, that they continued to do so over the next three years. He attributed the decreases to strengthened southwesterly winds in the southern Indian Ocean. Unfortunately, the measurements for 1897–1899 appear to have been lost. The decreases appear to have been caused by a northward movement of the Subtropical Front associated with a strong El Niño.

The Subtropical Front (STF) was identified during a survey in late February 1976 from 110–117°E that revealed that surface salinities decreased from 35.6 to 34.8 between 38°S and 39°S, with temperatures of 16 ± 0.5°C (Cresswell *et al.* 1978). In a comprehensive study Belkin & Gordon (1996) considered the STF to lie at about 39°S, well to the south of Western Australia. Using November 1994 data from the *Franklin* voyage FR9410, Schodlok *et al.* (1997) found the STF spans 39.4 – 40°S. Using satellite imagery Kostianoy *et al.* (2004) concluded that in July 1999 there were two STFs south of Western Australia, at 38°S and 39–40°S. James *et al.* (2002, p. 145) reported that for their study area south of Australia 'salinity

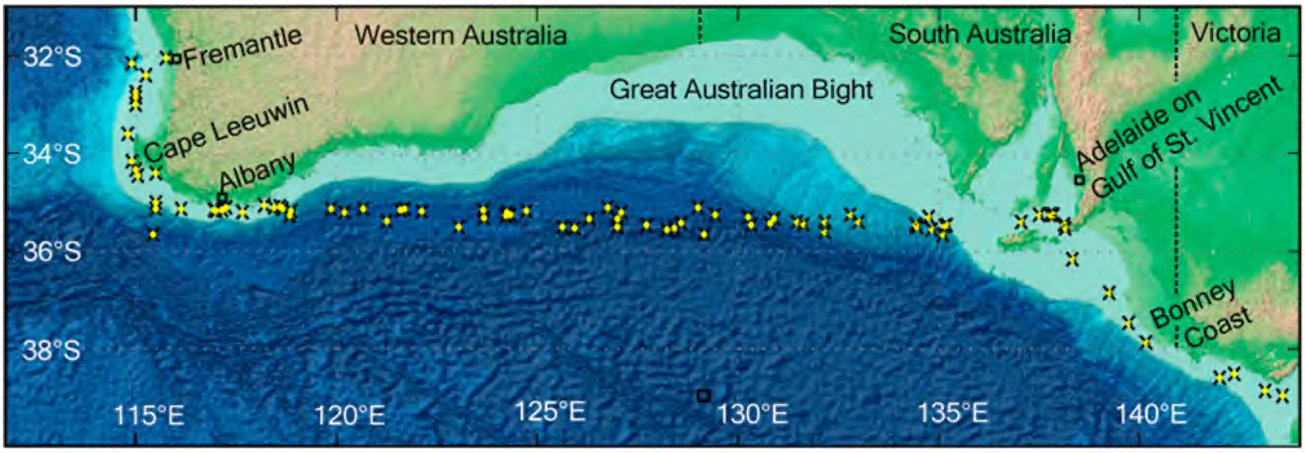

Figure 1. Chart showing all sampling points for temperature and salinity along the voyage paths between Fremantle, Adelaide and Victoria in May–June, July–August and November–December 1896. General Bathymetric Chart of the Oceans (https://www.gebco.net).

is at best weakly affected by seasonal change so that the horizontal salinity change associated with the STF usually reaches through the mixed layer'. They pointed out that the shallow (~50 m) mixed layer in summer prevents the surface expression of the characteristic 12°C isotherm. These observations show considerable ocean-current complexity south of Western Australia, as do the earliest satellite-tracked drifters and satellite sea-surface temperature measurements (Cresswell & Golding 1980; Legeckis & Cresswell 1981).

The two satellite images in Figure 2 cover a strengthening El Niño, with cold waters revealing that the STF can reach the 35°S parallel traversed by the merchant ships in 1896. The former from 18 November 1986 (Fig. 2a), with a Southern Oscillation Index (SOI) of -14, shows warm water carried southward and then eastward in the Leeuwin Current, with offshoots at 116.5°E, 118.5°E and, less obviously, at 120°E. There is a warm core eddy at 113–114°E that may have formed from a similar offshoot and drifted westward, as observed more recently (Cresswell & Griffin 2004). In the southeastern part of the image a 50-km wide band of cold water extends northwestward several hundred kilometres to 36°S, where it appears to be overrun by one of the offshoots. Features that could be identified on the edges of the cold band on this and the previous day showed movements to the northwest at 0.25 ms^{-1}. With a temperature of 13°C, this band suggests that it contains water normally found south of the STF with more cold water spreading northward to 35°S between 119°E and 121°E.

The satellite image for 6 March 1987 (Fig. 2b), with a SOI of -17 (strengthening to -24 in April), shows waters of 21°C at 32°S in the Leeuwin Current that finished near 34°S. Farther downstream to the east, ill-defined patches of 18.5°C water are possibly remnants of an earlier Leeuwin Current flow. A cool 17.5°C plume on the southern continental shelf emanating from between 116°E and 118°E was likely upwelling induced by easterly winds. The plume moved westwards to 33°S, progressively warming en route. This northward flow would later be called the Capes Current (Gersbach *et al.* 1999; Pearce & Pattiaratchi 1999). Cold water, perhaps

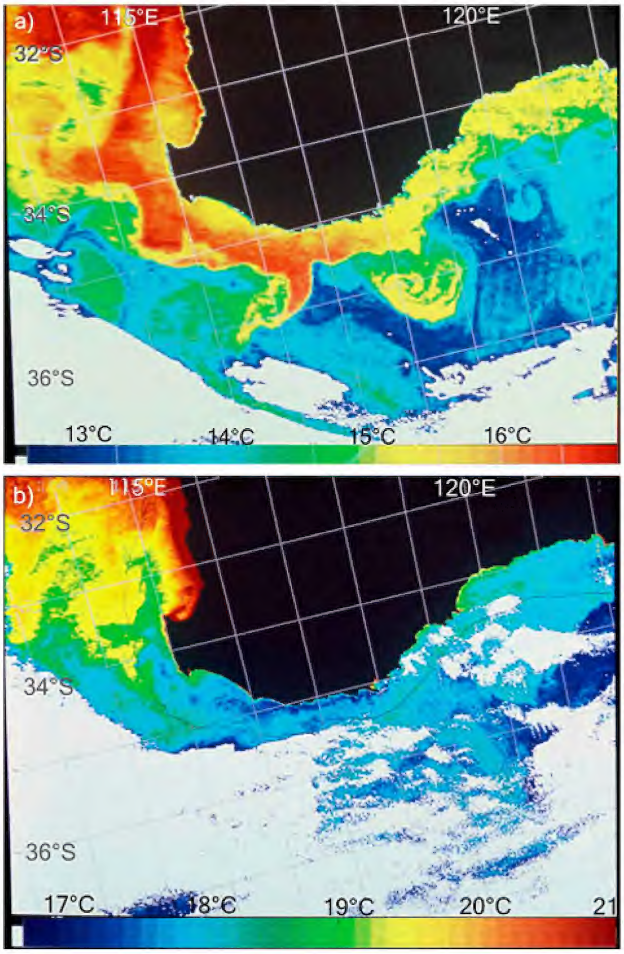

Figure 2. Satellite sea-surface temperature images from south of Western Australia: a) 18 November 1986; and b) 6 March 1987. The temperature scale is at the bottom of each image; clouds are white; a black mask has been put over the land; and there is a 1 x 1° latitude–longitude grid. Data from NOAA 9 satellite received by CSIRO in Hobart. 2b is from Cresswell & Peterson (1993, plate 1c).

related to a northward move of the STF, crossed 35°S near 122°E.

The dynamics and seasonality of the Leeuwin Current, the wind-driven upwelling current and the Flinders Current farther offshore, have been examined in detail by Akhir *et al*. (2020). The strong effects of El Niño and La Niña on the Leeuwin Current are evident in Lough *et al*. (2012, fig. 8) when compared with SOI values from the Bureau of Meteorology: La Niña drives a strong Leeuwin Current eastward along the southwestern Australian continental shelf edge whereas the Leeuwin Current is weaker during El Niño. Huang & Feng (2015) found that the extent of the Leeuwin Current's sea-surface temperature was reduced in El Niño years based on Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data.

METHODS

In Melbourne Fowler (1898, p. 688) measured the densities of the water samples, 'referenced to distilled water at 39.2° Fahr. as standard', at temperatures as close as possible to 60°F (15.6°C), the design temperature of the hydrometers. He took the mean of three different readings for each water sample and reported that individual readings differed from the mean by no more than 0.0006 gram cm^{-3} (0.6 kg m^{-3}). In addition, he checked his instruments in solutions of known densities.

Sea-water density was calculated from Fofonoff & Millard (1983) to back-calculate the surface salinities from Fowler's densities (at 15.6°C). These were cross-checked with the seawater density calculator (available at https://www.mt-oceanography.info/Utilities/density.html).

Although Fowler commented that errors may have been made with some temperature measurements due to thermometers being removed from buckets too soon, or through allowing sunlight onto them, the temperatures along repeated passages (Fig. 2) were usually not overly different. However, those on the eastbound passage between 22 and 28 August 1896 deserve further comment: the temperatures were unchanged at 58°F (14.4°C) for 5° of longitude from 120°E, and then unchanged at 56°F (13.3°C) for almost 10° of longitude from 128°E. This may have been due to crewmen not completely adhering to Fowler's instructions.

Fowler's 1896 data, particularly south of Western Australia, were compared with surface data from research voyages between 1976 and 2017 accessed through the CSIRO Oceans and Atmosphere web site https://www.cmar.csiro.au/data/trawler. Until the 1980s these were from the surface Nansen bottles from hydrology casts; for later voyages a subsample of the thermosalinograph data was used. Hourly sea level data for Fremantle were accessed from gesla.org, i.e. the Global Extreme Sea Level Analysis project.

RESULTS

Fowler's temperatures and derived salinities along ~35°S between Cape Leeuwin in the west and Victoria in the east for May–June, for July–August, and for November–December 1896 are summarized in Figure 3. The temperatures for the first two periods suggest that the ships were in the warm Leeuwin Current west of about 120°E. East of there the coast and Leeuwin Current trend northward and, as would be expected, cooler Southern Ocean waters were encountered. The

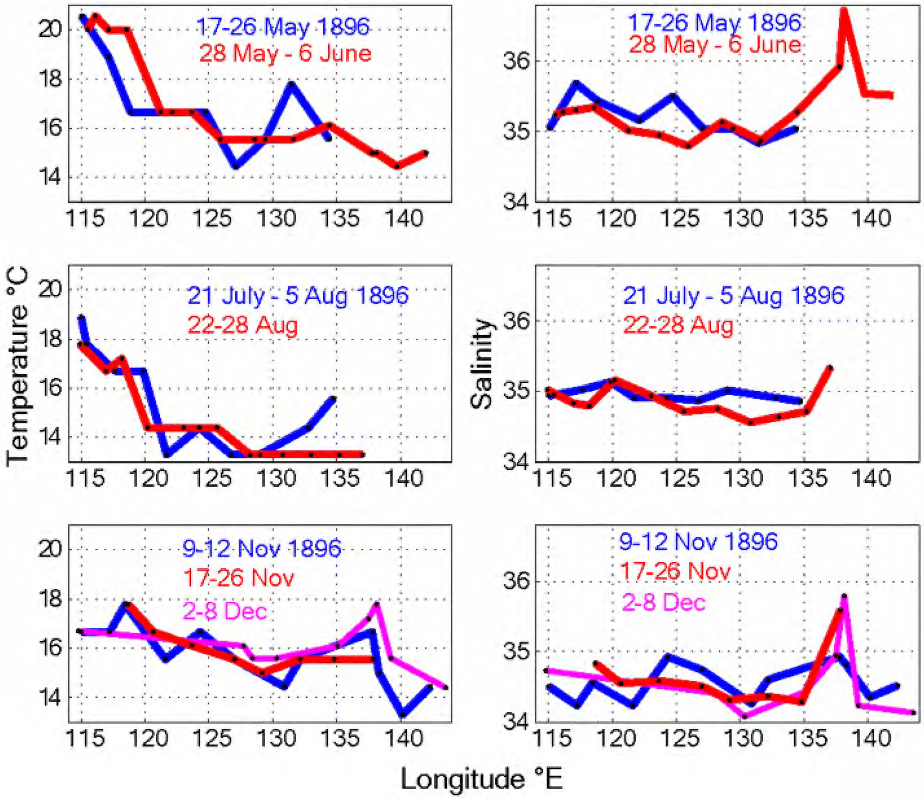

Figure 3. Temperatures (left) and derived salinities from seawater samples (right), taken on steamships in May–June, July–August, and November–December 1896. The red and magenta lines indicate eastbound passages and the blue lines for westbound. The two off-scale salinity values in St Vincent's Gulf in June (red) were 36.25 and 37.05; the off-scale salinity value in December (magenta) was 34.08.

November–December temperatures were low, <17°C in the west: possibly the result of an absence of the Leeuwin Current or wind-driven upwelling on the continental shelf immediately east of Cape Leeuwin (cf. Fig. 2b). At the same time, temperatures were as low as 13.3°C (with salinity 34.35) off the Bonney coast (140°E) of South Australia where there can be summer upwelling. The Bonney upwelling, and others that are part of the Great South Australian Coastal Upwelling System (Kämpf, 2015), occasionally take place in summer in response to coast-parallel southeasterly winds. The upwelling was first mentioned by Hynd & Robins (1967). Rochford (1977), Schahinger (1987), Kämpf *et al*. (2004) and Kämpf (2015) indicate upwellings can take place in December–March whereas Bye (1970) and Lewis (1981) suggest November–March. Whether or not there was an early upwelling in November 1896 cannot be determined with just one temperature measurement and no knowledge of the winds.

The high salinities in May–June from 115°E almost to 119°E, were probably due to the Leeuwin Current, consistent with the high temperatures there. In the shallow waters of St. Vincent's Gulf (138°E) the salinities were high, reaching 36.25 and 37.05 in May–June and a little over 36 in November–December (no data from July–August). Of particular interest is the overall decrease in salinity of roughly 0.6 over the 7-month period, in step with the decrease in density that Fowler commented upon. Note that the salinities in the west in November seem almost too low to be realistic, ranging from 35.2 to less than 34.6.

In the west in May–June (Fig. 4a, b) there is good agreement between the Fowler temperatures and those of *Franklin* in June 1987, but the Fowler salinities were lower by about 0.3. The Leeuwin Current was strong during the *Franklin* voyage (Cresswell & Peterson 1993) and was also evident in May–June 1896 (Fig. 3). The relatively high temperatures west of 120°E in both July–August 1896 and July 1994 (Fig. 4c, d) suggest the influence of the Leeuwin Current. Current measurements made during FR9407 showed the Leeuwin Current rounding Cape Leeuwin at up to 1 ms^{-1}, and that it progressively weakened eastward to end near the continental shelf edge (Cresswell & Domingues 2009). The near-shore high salinities found in the Great Australian Bight during this voyage were probably due to evaporation, which may also explain the cold salty waters in the shallow St. Vincent's Gulf.

The November 1896 measurements do not show a Leeuwin Current and the salinities were the lowest for the year (Fig. 3). In contrast, measurements from RV *Franklin* in November and December 1994 and RV *Investigator* in November 2017 (Fig. 4e, f) suggest that the warm, salty Leeuwin Current flowed eastwards after rounding Cape Leeuwin. Incidentally, the waters adjacent to the continent west of about 121°E were saltier in 1994 (*Franklin*) than in 2017 (*Investigator*). Farther south, the sub-Antarctic waters were cooler and fresher. From their analyses of data collected along 120°E on FR9410, Schodlok *et al.* (1997) concluded that the STF lay at 39.4 – 40°S with temperatures of 12.7 – 14.8°C and salinities of 34.81 – 35.48. Surface-water temperatures during the *Diamantina* voyage from 37–40°S in late February 1976 were relatively high, probably due to insolation and the formation of a mixed layer in summer, and perhaps a southward offshoot of the Leeuwin Current.

The ellipses around the Fowler temperature–salinity (T–S) values in Figure 5 show how the salinities decreased during 1896, and that the values were scattered compared with those from the more recent voyages. For the mean of the T–S values of November–December 1896 (Fig. 5c) to match those of the *Franklin* and *Investigator* voyages would require an average salinity increase from 34.6 to 35.6, or an average temperature decrease from ~16.5°C to 9.5°C. Another approach is to examine the latitude colour coding: the November–December 1896 salinities at ~35°S were found ~10° of latitude farther south during the *Franklin* and *Investigator* voyages.

The T–S data from *Diamantina* comes close to the Fowler data (Fig. 5c) and were only 2–5° of latitude south of 35°S; the surface waters would have warmed over summer. *Diamantina* reached the STF and crossed both a cyclonic eddy and a larger anticyclonic feature (Cresswell *et al.* 1977). This raises the question whether the STF moved northward to 35°S during 1896 bringing with it cool, relatively low salinity waters.

DISCUSSION

Fowler's measurements of temperature and density between southwestern Australia and Victoria yield some intriguing findings when compared with modern data, accepting that the crewmen taking the water temperatures did as good a job as conditions permitted. Fowler's density measurements on the water samples back in Melbourne with hydrometers and temperature near 60°F (15.6°C) were certainly rigorous given that he took the means of three readings and that he honed his skills with more than a year of observations at the Sorrento Back Beach. Applying the UNESCO formulae to calculate salinities from the densities, the November 1896 values at the western end of the passages were low and, in combination with their temperatures, seem unrealistic for that region. This is explored as follows:

(1) **Albany and Rottnest stations**. At the Albany 50 m hydrology station, which operated in 1978–1983, surface salinities ranged from 35.2 to 36. These values barely overlap those for November 1896 (34.55 – 35.25). Data collected from over four decades at the Rottnest Island 50 m hydrology station (near the continental shelf edge at 32°S, west of Fremantle) reveal salinities of 35.15 – 36.15 with a typical annual variation of 0.3 – 0.6, although the La Nina of 1973–75 brought the salinities down to 35.2 – 35.5.

(2) **Rainfall as a factor**. Rainfalls at Albany, Bunbury and Fremantle were not markedly different in 1896 from several years before and after (http://www.bom.gov.au/metadata/catalogue/19115/ANZCW0503900430), and so seems unlikely to explain salinity variations.

(3) **The Southern Oscillation Index and the Subtropical Front**. The strong El Niño that commenced in 1896 may have led to a weaker Leeuwin Current, thereby allowing the STF to move northward, bringing with it cooler, fresher waters towards the 35°S path of Fowler's merchant ships.

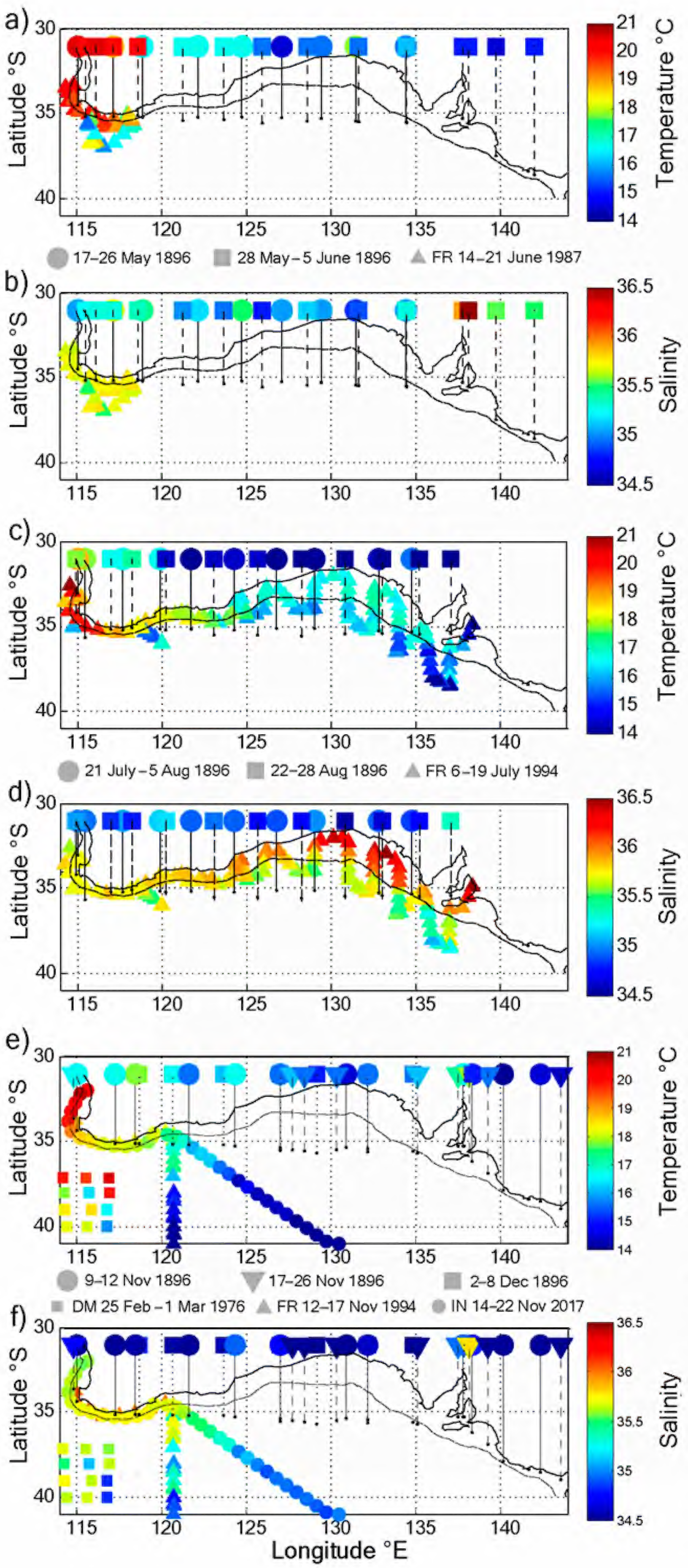

Figure 4. Fowler's 1896 temperature and salinity surface measurements colour coded as large symbols offset to 31°S compared with measurements from modern voyages: a) and b) Fowler values for May–June 1896 and modern values from RV *Franklin*; c) and d) Fowler values for July–August 1896 and modern values from RV *Franklin*; and e) and f) Fowler values for November–December 1896 and modern values from HMAS *Diamantina*, RV *Franklin*, and RV *Investigator*.

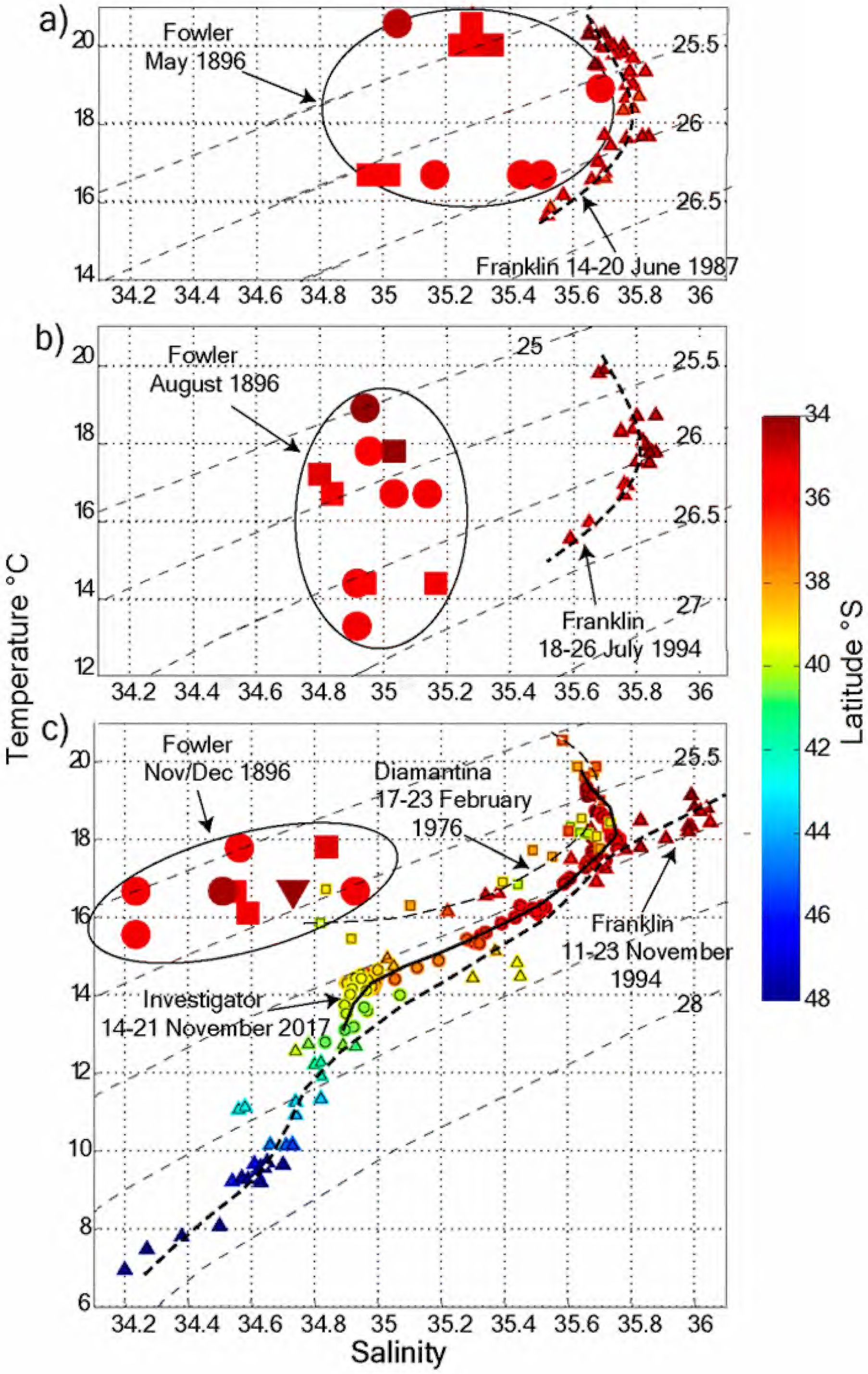

Figure 5. Temperature–salinity diagrams colour coded for latitude. The angled dashed lines are isopycnals. The Fowler data from 114–125°E have circles for westward passages and squares and a triangle for eastward ones. Small symbols mark recent surveys as follows: a) RV *Franklin* from 33–37°S, 114–119°E (triangles); b) RV *Franklin* from 32–38.5°S, 115–125°E (triangles); and c) RV *Franklin* southward from WA to 48°S (triangles); HMAS *Diamantina* from 37° to 40°S (squares); and RV *Investigator* southeastward from WA to 41°S (circles).

El Niño and La Niña events are defined by SOI values sustained at less than -7 and greater than +8, respectively. Over the past 150 years the most significant El Niño events commenced in May 1896 and May 1905 with SOI values of -42.2 and -42.6 respectively. For comparison, El Niños in 1953, 1983 and 1997 had values of -31.9, -33.3 and 24.1. The SOI associated with the 1896 El Niño (Fig. 6) took 18 months to return to zero and through to the end of 1899 only exceeded the +8 for a La Niña on seven occasions, and was not sustained. Fremantle sea level was first recorded in January 1897 and so missed the onset of El Niño in 1896; sea level was relatively low in 1897 and 1899, and high in 1898.

Fremantle sea level, when interpreted through the analyses of Feng *et al.* (2003) covering 1950–2000, suggest an El Niño was in progress in 1897 (Fig. 7), in accord with the low values of SOI. The Leeuwin Current would have been weaker, and, perhaps, almost absent south of Western Australia—as implied by the extremely low values of SOI in 1896. Zinke *et al.* (2014, fig. 4b) reconstructed Fremantle sea level from the analysis of coral core samples from the Houtman Abrolhos Islands at 28.3°S and plotted these with the observed sea level at Fremantle. Even though there are no observations before January 1897 it is likely that the reconstructed sea level was low in 1896, as would be expected from the strong El Niño.

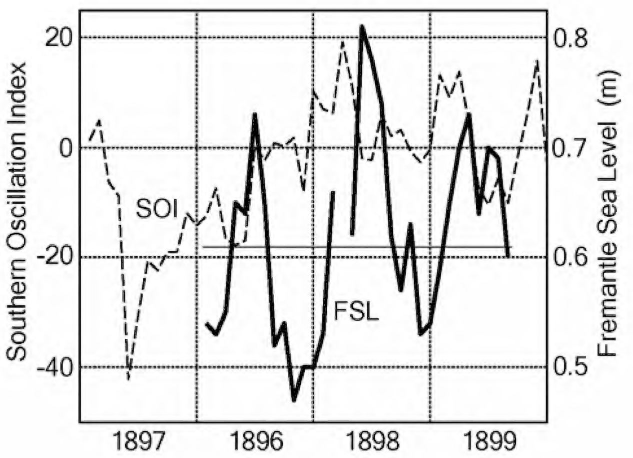

Figure 6. The Southern Oscillation Index for 1896–1899 (dashed line) and Fremantle monthly mean sea level from January 1897 (gesla.org), when recording began, to August 1899. There is a gap in the data for March 1898. The thin line at 0.61 m marks mean sea level for the late 1890s (from Pattiaratchi & Eliot 2009).

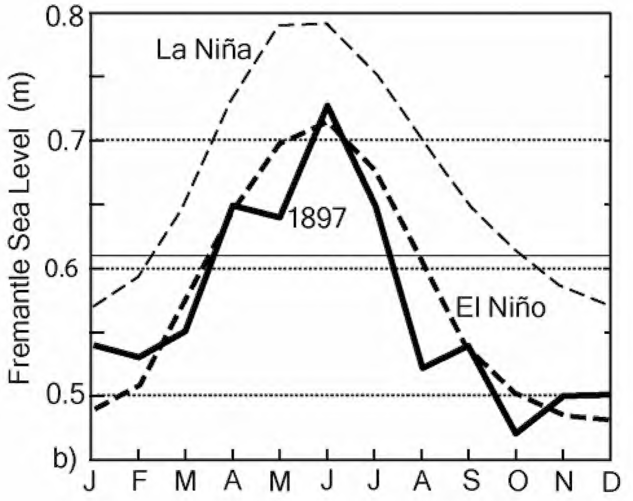

Figure 7. Monthly mean sea level at Fremantle (thick line) calculated from gesla.org for 1897 and the mean sea level of 0.61 m for the late 1890s. The dashed lines show the deviations from mean sea level for el Niño and la Niña events between 1950 and 2000 from Feng *et al.* (2003, fig. 15). Mean sea level for those years has been superimposed on the 0.61 m mean sea level for the late 1890s; the sea level scale is the same.

If the STF had moved northward in 1896 then the low salinity waters that it brought would have been largely conserved, whereas insolation may have raised the sea-surface temperatures to match those measured by Fowler. The puzzle remains and, if anything, it is made more enticing with Fowler (1901) reporting, but only in an abstract and without giving values, that water densities and temperatures off southern Australia continued to decrease through to 1899.

CONCLUSIONS

- Temperature measurements reveal the Leeuwin Current south of Western Australia in May–June and July–August 1896.
- A northward move of the Subtropical Front, linked to a very strong El Niño and a weak Leeuwin Current, is the likely cause of decreasing salinities and temperatures south of Western Australia measured during 1896 and 1898.
- All water samples from St. Vincent's Gulf were highly saline due to evaporation, in agreement with present-day knowledge.

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Matching theories on kleptoparasitism to a complex avian event in Perth, Western Australia

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Theories on kleptoparasitism are matched to a complex event during which a Laughing Dove *Streptopelia senegalensis* was injured by a car, probably fatally, then depredated by a group of Australian Magpies *Gymnorhina tibicen* and subsequently kleptoparasitized by two Australian Ravens *Corvus coronoides*. Relevant phylogenetic and ecological theories on kleptoparasitism suggest the main factors in play included the ravens' greater size and intelligence (estimated using an encephalization quotient); the prey type being a vertebrate that provides a rich energy source; their prey handling times, which the ravens minimised to their advantage; and the context of an open urban habitat, which facilitated clear observations for the ravens and the magpies.

Keywords: passeriformes, urban, road, terrestrial, corvidae

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INTRODUCTION

Kleptoparasitism is the theft of food already procured by others and can be intraspecific or interspecific (Brockman & Barnard 1979). Kleptoparasites, like predators, are common in both terrestrial and aquatic realms, and amongst vertebrates and invertebrates (Iyengar 2008). However, this paper focuses on terrestrial Aves (birds), with an emphasis on examples from the Passeriformes (Perching Birds) and Corvidae (Songbirds). Kleptoparasitism in birds appears to be a labile evolutionarily trait (Morand-Ferron *et al*. 2007) that is present in some groups more than others; for example, there is a disproportionate number of kleptoparasitic taxa in Laridae (Gulls, Terns), Fregatidae (Frigate birds) Accipitridae (Eagles, Kites and Goshawks) and Corvidae (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007).

Some of the central conditions required for kleptoparasitism include the value of the stolen resource must exceed the costs of the theft, including the cost of the competition (Iyengar 2008). Typical attributes in kleptoparasites are size, greater cognitive ability and aggressiveness (Morand-Ferron *et al*. 2007). In particular, they must have the ability to learn (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007). Species vary in the extent that they adopt kleptoparasitic behaviour. Some use it exclusively (obligate kleptoparasites), whereas others adopt its use optionally or discretionarily (facultative kleptoparasites; Iyengar 2008). Facultative kleptoparasites are usually dietary generalists and opportunists (Barnard 1984; Iyengar 2008). Conversely, hosts typically have a diet including vertebrates, because such prey is energy rich and often requires long handling times (Brockman & Barnard 1979; Morand-Ferron *et al*. 2007).

In addition to the intrinsic requirements of the thieves and hosts, suitable ecological conditions facilitate food theft. Open environments such as two-dimensional grasslands or marine habitats provide greater visibility than closed forests, thus increasing the potential to observe hosts (Morand-Ferron *et al*. 2007). Another factor is the social foraging environment; for example, the multi-species combinations of seabirds (Furness 1987) or heterospecific social foraging groups that share the same foraging habitat (assemblages), which allows group members to observe how conspecifics and heterospecifics forage. In such locales it is obviously beneficial to see the foraging success of others (Brockman & Barnard 1979).

This paper reports a complex, single event incorporating road-injury, predation and kleptoparasitism, and involving three passerine and one non-passerine species. The kleptoparasitism is the main focus of the paper. The event is compared to theories derived from comparative analyses and reviews on kleptoparasitism. Overall, the events observed match theoretical predictions.

METHODS AND RESULTS

Rationale

In order to explain the observed predation and subsequent theft, aspects of each species morphology, behaviour and ecology, along with the urban habitat are related to current theories on kleptoparasitism. An estimate of each species' cognitive ability, i.e. an encephalization quotient (EQ), was calculated from the body mass and brain mass of each species (Table 1). The EQ of each was then assessed to see if it aligned with general theories on kleptoparasitism. Absolute, rather than relative, brain size is considered the best predictor of cognitive capacity (Olkowicz *et al*. 2016). Taxonomy used

Table 1. Encephalization quotient (EQ*) of the four species.

Species	Body mass (gm)	Brain vol. (ml)	EQ
Australian Raven	675	9.83	1.11
Australian Magpie	317	4.65	0.87
Magpie-lark	92	1.68	0.71
Laughing Dove	101	1.24	0.49

*calculated by the ratio of the absolute brain volume to the volume expected for its body size (i.e. bodysize$^{2/3}$):

absolute brain volume / 0.12 × body mass $^{0.66}$ (Jerison 1973).

Species masses are in grams and taken from Dunning (2008).

Brain volume in millilitres from (Iwaniuk & Nelson 2003).

follows Jønson *et al.* (2020). Encephalization is a proxy for intelligence or cognitive ability allowing comparisons between different species with the majority of studies using the encephalization quotient (Mitchell 2016). The encephalization quotient adjusts for disparate taxonomic group using a cephalization factor (0.12 was used in this study; Jerison 1973).

Species backgrounds

The four species involved in the event described below are common to urban settings in Perth, including the locality involved. All four have benefitted in various ways from the changes associated with urbanisation.

The Laughing Dove *Streptopelia senegalensis* is a non-native, granivorous bird, introduced to Western Australia in 1898 (Serventy & Whittell 1976; Johnstone & Storr 1998). Australian Magpies *Gymnorhina tibicen* (hereafter magpies) are well-known opportunists, known to take small birds when the opportunity arises (Fulton 2006), although they are predominately insectivorous feeding mostly on the ground (Floyd & Woodland 1981; Johnstone & Storr 2005). They are highly social birds often seen in groups (Higgins *et al*. 2006), though individuals privately cache food (Rollinson 2002). Australian Ravens *Corvus coronoides* (hereafter ravens) share ground foraging attributes with the magpie, though not entirely. Ravens are broadly omnivorous and generalist carrion feeders; they have benefitted from dead livestock and roadkill (Rowley & Vestjens 1973), as well as scavenging from roads and natural refuges within urban environments (Sazima 2020). Ravens exploit human refuse in densely urbanised areas, showing the capacity to forage more innovatively than other species (Diquelou *et al*. 2016). The Magpie-lark *Grallina cyanoleuca* is granivorous and insectivorous including taking freshwater invertebrates. It feeds predominately on the ground and around water (Johnstone & Storr 1998), and is one of the most successful adapters to urban environments (Kitchen *et al*. 2011).

The observation

In a southern suburb (at 32°20′31.2″S 115°45′44.9″E) of Perth, Western Australia, on 28th April 2014, a Laughing Dove (hereafter dove) was dazed and injured by a passing car. Three Australian Magpies *Gymnorhina tibicen*, from a larger group, attacked the dove as it staggered and fell several times on the road. The magpies pecked the dove's head apparently trying to kill it. Despite the continued pecking it kept struggling and falling, apparently unable to fly. One magpie carried the still alive dove for more than 10 m dropping it on a grassy nature strip and then continued to peck it. A Magpie-lark watching the attack from about 1.5 m away did not attempt to peck the dove, but seemingly waited for an opportunity to do so—the Magpie-lark appeared excited based on its jizz and springy or bouncing movements. Two ravens arrived and watched the dove being carried off the road. At the point when it seemed that no fight was left in the dove, and while the magpies continued to peck, the two ravens approached in stages over approximately 30 seconds. They then flew the final 5 m directly to the disabled dove, stopped and looked briefly at the magpies before taking it from them. The two ravens flew with the dove (one carrying) to a point about 25 m away, then commenced eating it while it was still alive. At this stage I approached for a better view—they may have been aware of me as they then took the dove farther away, although it may be that removing the dove lessened the chances of combat with the magpies. The ravens took the injured dove over a 2.5 m high fence about 5 m from where they had been and continued to pull it apart. The same Magpie-Lark that had approached while the magpies had the dove on the road and again on the grass verge followed the ravens with the dove, whereas the magpies did not. The Magpie-lark did not consume or make contact with any part of the dove, yet it looked as though it wished to join the kill or at least snatch some of the dove.

DISCUSSION

Brain versus brawn

The core of this observation was that two ravens stole a valuable energy-rich resource, which had been the opportunistic prey of the three magpies. This theft might be considered unexpected given that magpies can be aggressive and predatory towards other birds—Fulton (2006) describes magpies killing a Brown Goshawk *Accipiter fasciatus* in brood defence—and are well-known for attacking humans (e.g. Warne *et al*. 2010). The magpies outnumbered the ravens, but individually the mass of a magpie is about 47% of a ravens. Thus, the physical size of the participants suggests that the ravens would be victorious in competition for the dove. However, in a targeted review, Morand-Ferron & Lefebvre (2007) found that the residual brain size was significantly greater in kleptoparasites than their hosts, but body mass was not. Thus, brains and not brawn better explains kleptoparasitism. In the example described the ravens had both a greater body mass and absolute brain volume than the other birds. Consequently their greater brain-to-body ratio, and therefore greater encephalization quotient, suggests a cognitive ability above that of the others. This study found that ravens were more intelligent than the other species, and is supported by a recent urban study measuring innovative foraging, in which ravens outperformed all other measured species by using a greater number of skills that require greater cognitive ability (Diquelou *et al*. 2016).

Although it is counter-intuitive to dismiss that size plays a part, it is accepted that greater cognitive ability increases the probability of success (Morand-Ferron & Lefebvre 2007). In the observed event the raven's greater mass probably helped in securing the dove from the magpies. Fulton (2019) derived a predator-prey mass ratio of 0.25 for nest predators and their prey, using the mean size of adults at prey-nests. In the same study, borrowed data on raptor prey from Olsen *et al*. (2010) indicated a mean predator-prey mass ratio of 0.26. These show that the prey were 75% smaller than the predators. Therefore, it seems likely that greater body mass and cognitive ability both contributed to the ravens taking the dove from the magpies.

Finding and handling prey

Hosts that catch and handle prey are adding value for the thief (Morand-Ferron & Lefebvre 2007; Iyengar 2008). The magpies (the host) invested energy into catching and preparing the dove for consumption, but in doing so added to the prey's value for the thieves (the ravens). The characteristic sequence of predation events is typically: the prey is searched for, acquired and handled, and then consumed after sufficient handing. In that sense, the sequence progressively adds value to the prey. Thus, the thief gains greater benefit from taking the prey later in the handling stage (Hadjichrysanthou *et al*. 2018). This is exactly how the ravens behaved in the event described, i.e. they maximised their benefit (and minimized their efforts) by delaying the theft.

Vertebrate prey and phylogeny

Large prey that require greater handling times are favoured by and are more profitable to kleptoparasites (Iyengar 2008). Host species are usually characterised as frequently preying on vertebrates (Morand-Ferron & Lefebvre 2007). By comparison, kleptoparasites are commonly considered predatory and dietary opportunists (Brockmann & Barnard 1979). Predators familiar with finding and handling vertebrate prey are thought to be pre-adapted to kleptoparasitism (Brockmann & Barnard 1979). Brockmann & Barnard (1979) further highlighted that almost all kleptoparasitic bird families were predators that included vertebrate prey in their diet. They indicate that the Accipitridae, Laridae in the non-Passeriformes and Corvidae in Passeriformes have significantly more kleptoparasites than other families. In Australia, there are few reports of kleptoparasitism in Passeriformes, although the few that have been published are concentrated within the Corvidae and Artamidae, and the thieves were considered more facultative than obligate (Lepschi 1990; Robinson 1993; Fulton 2005; Recher & Davis 2005). Furthermore, Krohn (2016) highlighted *Corvus* species as kleptoparasites including the Australian Raven. Many members of this family (Corvidae) are kleptoparasites due to their cognitive superiority to most other birds (Emery 2006). In addition, they have forebrain neuron counts equal to or greater than primates with much larger brains (Olkowicz *et al*. 2016).

Conspicuousness of vertebrate prey

As discussed above vertebrate prey are associated with kleptoparasitism by providing more energy and by being conspicuous. They are large, mobile and take longer to handle, which makes them conspicuous to kleptoparasites (Morand-Ferron & Lefebvre 2007). With three magpies undertaking the handling of the dove, they were conspicuous enough to attract the ravens, the Magpie-lark and myself. The stumbling of the dove, after being hit by a car, was undoubtedly the initial stimulus presenting a conspicuous image on a featureless surface—the road. The presence of car and magpies is commonplace; without the image of the injured dove such things would pass without being noticed.

CONCLUSION

A group of factors interacted in this short event. The open environment of the road facilitated kleptoparasitism, by making its events conspicuous. The prey was a rich energy source making it valuable enough to steal. Ravens and magpies share the same social habitat within the same assemblage. The ravens were the largest and most intelligent bird in this group, their greater intelligence fitting the contemporary theory that kleptoparasites are more intelligent than their hosts. I suspect that urban birds will continue to be killed or injured in this manner, so such events must be more commonplace than has been reported.

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Lower Permian (Sakmarian) palynoflora from the Woolaga Limestone Member of the Holmwood Shale, northern Perth Basin, Western Australia

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Abstract

The Woolaga Limestone Member—a thin, muddy, calcareous unit of the Holmwood Shale in the northern Perth Basin of Western Australia—contains a diverse and exceptionally well preserved palynoflora associated with a varied marine invertebrate fauna indicative of a Sakmarian (Early Permian/Cisuralian) age. Spores and pollen grains are overwhelmingly predominant in this palynomorph assemblage, with the identified taxa suggesting its assignment to either the *Converrucosisporites confluens* Zone or the succeeding *Pseudoreticulatispora pseudoreticulata* Zone of the currently recognized Western Australian Permian palynozonation. The spore-pollen content reveals substantial allochthonous contributions from the pteridophytic and gymnospermous (notably glossopterid) land vegetation into the marine depositional environment. Autochthonous or near-autochthonous components consist of algal microfossils (marine, fresh water, or brackish water) and rare scolecodonts (wholly marine).

Keywords: palynology, Lower Permian, Perth Basin, Western Australia

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INTRODUCTION

The past century has witnessed progressive and substantial developments in palynological studies, particularly, but by no means exclusively, in a range of geological and palaeobotanical enterprises, and applications. Whereas marine invertebrate faunas are prime requisites for the precise dating of stratal successions in terms of the international timescale, palynological microfossils (palynomorphs) are typically crucial in establishing correlations between non-marine and marine facies.

The Permian system is represented in Australia by both fossiliferous marine and palyniferous terrestrial successions. Many of the latter are coal-bearing such as in Western Australia's Perth and Collie basins, and in the Sydney and Bowen basins of eastern Australia. The highly weathered nature of the Australian terrain tends to militate against establishing marine to non-marine stratigraphic/chronological correlations because palynomorphs have proven highly susceptible to destruction by the oxidative weathering in the Cenozoic. Hence Australian palynologists necessarily rely almost entirely on samples from boreholes (e.g. Jones & Truswell 1992) or from strata exposed below the level of lateritization (e.g. Playford 2019). In that regard, the present study is a conspicuous and fortuitous exception: the samples hosting the palynoflora recorded herein are from outcrop—seemingly, timely cementation of the hosting sediment effectively militated against subsequent deleterious weathering.

GEOLOGICAL SETTING

The Woolaga Creek area is situated in the northern Perth Basin, specifically within the Irwin Sub-basin (aka Irwin Basin or Irwin Terrace) between the Darling and Urella faults (Fig. 1), and represents a southerly extension of the Permian succession exposed along the Irwin River (Playford 1959; Playford *et al.* 1976; Cockbain 1990; Mory *et al.* 2005; Mory & Haig 2011). In both areas, the Permian strata comprise the following essentially conformable lithostratigraphic units (Fig. 2): in ascending order, Nangetty Formation (glacigene, marine and continental), Holmwood Shale (cold- to warm-water marine), High Cliff Sandstone (marginal marine), Irwin River Coal Measures (non-marine, fluviodeltaic–paralic), Carynginia Formation (shallow marine, restricted circulation) and Wagina Sandstone (non-marine, fluvial).

The Holmwood Shale, as exposed in the western part of the Woolaga Creek area, consists predominantly of grey siltstone and mudstone with intercalations of thin lenticular bioclastic calcarenites. The age of the formation is well established as Cisuralian, specifically Sakmarian, on the basis of its invertebrate fauna. The formation's thickness, as reported by Playford (1959) at Woolaga Creek, is at least 132.6 m, its contact with the underlying Nangetty Formation being unexposed. Farther north, in the Irwin River area, limestone beds are fairly common within the Holmwood Shale (e.g. Beckett and Fossil Cliff members, of the lower and uppermost Holmwood Shale, respectively), but these are somewhat lesser developed in the less complete Woolaga Creek section. There the most conspicuous and fossiliferous calcareous unit forms a bouldery exposure—approximately 1 m thick and about 55 m below the top of the Holmwood Shale—termed the Woolaga Limestone Member (Playford 1959).

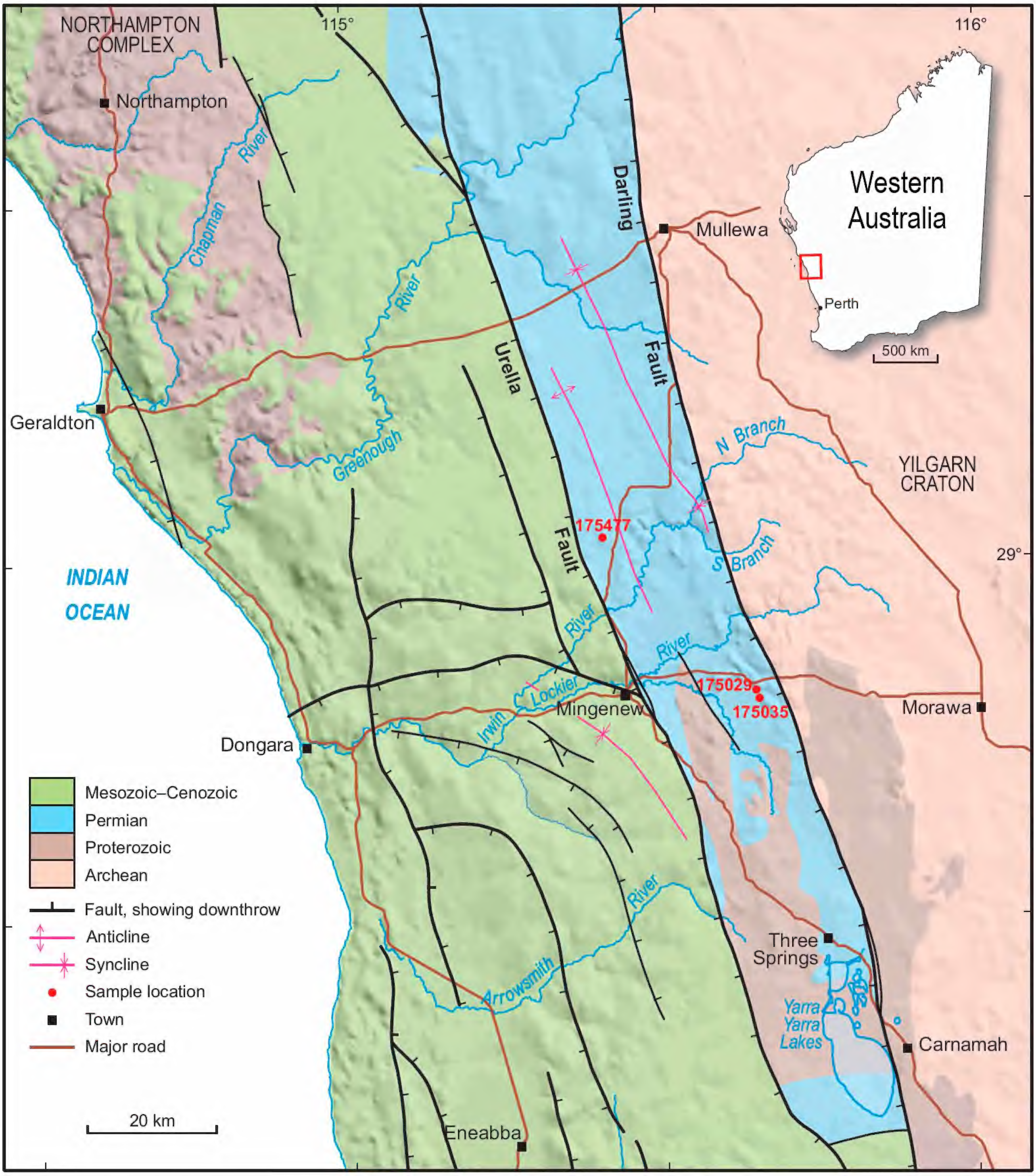

Figure 1. Locality map, northern Perth Basin, including locations of samples studied (UWA 175029, 175035, 175477).

The varied marine invertebrate fauna of the Woolaga Limestone Member includes foraminifers, scyphozoans, bryozoans, brachiopods, bivalves, gastropods, nautiloids, ammonoids, conulariids, annelids, ostracods, sponge spicules and serpulids (Playford 1959, Playford *et al.* 1976, Skwarko 1993, D.W. Haig, email comm., 2 June 2021). Of these, the ammonoid species *Juresanites jacksoni* (Etheridge Jr 1907), *J. campbelli* (Teichert & Glenister 1952) and *Svetlanoceras irwinense* (Teichert & Glenister 1952; previously known as *Uraloceras irwinense*) have been regarded as signifying a Sterlitamakian (late Sakmarian) age (Glenister & Furnish 1961; Glenister *et al.* 1990). Note that in a paper written five years prior to Glenister *et al.* (1990)—but not published until eight years later—Glenister *et al.* (1993, p. 55–56) indicated the likelihood of a Tastubian (early Sakmarian) age for the Woolaga Limestone Member. They further surmised that the Fossil Cliff Member could be late Tastubian but

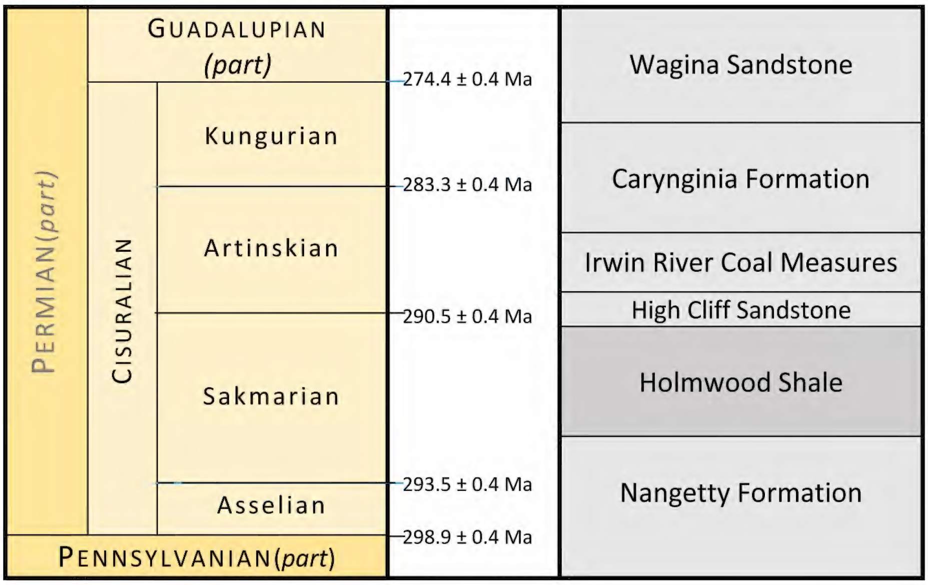

Figure 2. Permian stratigraphic succession, Irwin Sub-basin, northern Perth Basin. Ages of stage boundaries (in Ma) after Gradstein *et al.* (2020).

that 'for practical purposes the Tastubian–Sterlitamakian boundary is considered to lie at the base of the Fossil Cliff Member.' However, such suggestions were evidently negated by the 1990 publication in which Glenister and his colleagues reverted to a Sterlitamakian age for the Woolaga Limestone Member (and for the Callythara Formation in the Southern Carnarvon Basin).

Leonova (1998, 2011) indicated a generalized (undivided) Sakmarian age for the Western Australian Permian faunas that include *Juresanites jacksoni* and *Svetlanoceras* (*Uraloceras*) *irwinense*, which she equated with the Urals species *J. kazachorum* and *U. simense,* respectively (Leonova 2011, table 2.1.3). More recently, Leonova (2018) concluded that globally beyond the South Urals region 'it is impossible to recognize separate Early Sakmarian and Late Sakmarian [ammonoid] assemblages.'

A recent proposal of an older Permian (Asselian) dating for the Holmwood Shale (Backhouse & Mory 2020) is evidently based on tenuous extrapolation of palynological information and absolute age determination from northern Australia. This is discussed further in the correlation section of the present paper. From the above ammonoid evidence, a Sakmarian (likely Sterlitamakian) age is accepted for the Woolaga Limestone Member.

MATERIAL AND METHODS

This paper reports the palynofloral composition of two Woolaga Limestone Member samples collected on 5 September 2016 by D.W. Haig and A.J. Mory from the unit's type locality, at 29°12′12.7″S 115°39′17.7″E (sample UWA175029) and 29°11′53.5″S 115°39′13.7″E (sample UWA175035). Both samples are recorded as well-cemented, dark grey, fossiliferous, calcareous mudstone (D.W. Haig, email comm., 5 April 2021). A third sample (UWA175477; a muddy limestone), collected subsequently (2 May 2019) by D.W. Haig and A. Dillinger farther north (Macaroni Hill bioherm at 28°58′17.8″S 115°24′25.56″E) proved essentially non-palyniferous.

As noted previously, the two palyniferous surface samples (UWA175029, UWA175035), are unusual in an Australian context, particularly in yielding palynofloras with such fine and advantageous preservation. The following is a summary of the laboratory procedures (D.J. Mantle, email comm., 9 April 2021) employed by MGPalaeo in extracting and concentrating the palynomorphs: 'Just over 100 g of each sample were processed using acid-digestion palynological processing techniques as outlined by Phipps & Playford (1984), Wood *et al.* (1996) and Brown (2008). Following washing and crushing of the samples, 100 ml of 32% hydrochloric acid were added, for two hours, to remove carbonates. The resultant residues were then neutralized before the addition of 100 ml of 48% hydrofluoric acid, for 48 hours, to digest silicate minerals. The remaining residues were again neutralized, and then sieved using both 10 μm and 100 μm nylon sieves to remove the fine and coarse components, respectively. The residual organic material was then subjected to heavy-liquid separation using lithium heteropolytungstate (specific gravity 2.1), prior to mounting part of these kerogen fractions on glass microscope slides using Petropoxy-154. The remaining kerogen fractions were then subjected to 40 seconds' oxidation with nitric acid (69%), with further microscope slides being mounted of these oxidized assemblages. The UWA175035 sample initially yielded a very sparse but well-preserved assemblage; it was thus reprocessed to obtain improved spore-pollen specimens for study. For this repeat processing, the hydrofluoric (HF) acid digestion was increased to five days, with the HF acid refreshed daily. This long-digestion HF treatment resulted in significantly improved spore-pollen yields from this sample.'

The palynomorphs illustrated in Figures 3–9 were captured as high-resolution (TIFF) images with an Olympus BH2 binocular microscope, using either a 40× or a 60× oil-immersion objective, with attached Olympus DP26 digital camera. The images were acquired using Olympus cellSens® software and the plates were assembled via CorelDRAW graphics suite.

Table 1. Composition of palynoflora from the Woolaga Limestone Member arranged in major groups showing relative abundances (based on systematic counting of 250 specimens), figure numbers, and previously recorded occurrences from the Holmwood Shale.

Taxa		**Figure nos**	
Spores			
Apiculiretusispora sp. 1	•	4A/B	
Apiculiretusispora sp. 2	r	4C/D	
Brevitriletes cornutus (Balme & Hennelly 1956) Backhouse 1991	c	3S, T	* ✓
Calamospora sp.	r	3D	
Converrucosisporites confluens (Archangelsky & Gamerro 1979) Playford & Dino 2002	u	3I/J–L	* ✓
Converrucosisporites micronodosus (Balme & Hennelly 1956) Playford & Dino 2002	u	3G/H	* ✓
Converrucosisporites naumoviae (Hart 1963) Backhouse 1991	r	3M	* ✓
Densoisporites solidus Segroves 1970	c	4K/L	* ✓
Diatomozonotriletes townrowii Segroves 1970	r	4E, F/G	* ✓
Diatomozonotriletes sp. cf. *D. saetosus* (Hacquebard & Barss 1957) Hughes & Playford 1961	•	4H	
Diatomozonotriletes sp.	r	4I/J	
Gondisporites bharadwajii Foster 1979	•	4N	*
Gondisporites ewingtonensis Backhouse 1988	u	4Q, R	
Gondisporites wilsonii Backhouse 1988	r	4O/P	✓
Granulatisporites austroamericanus Archangelsky & Gamerro 1979	u	3N	
Horriditriletes curvibaculosus Bharadwaj & Salujha 1964	u	3P	
Horriditriletes ramosus (Balme & Hennelly 1956) Bharadwaj & Salujha 1964	u	3Q, R	* ✓
Indotriradites niger (Segroves 1970) Backhouse 1991	u	4M	
Kendosporites striatus (Salujha 1965) Surange & Chandra 1974	•	5P	
Laevigatosporites sp.	r	8A	
Leiotriletes badamensis (Venkatachala & Kar 1965) Foster 1975	r	3C	*
Leiotriletes directus Balme & Hennelly 1956	a	3B	* ✓
Microbaculispora tentula Tiwari 1965	u	3O	* ✓
Punctatisporites gretensis Balme & Hennelly 1956	r	3A	* ✓
Secarisporites lacunatus (Tiwari 1965) Backhouse 1988	u	4S/T, 5A	
Waltzispora sp.	•	3E, F	
Pollen grains			
Alisporites sp.	r	7F	
Barakarites rotatus (Balme & Hennelly 1956) Bharadwaj & Tiwari 1964	r	5B	*
Barakarites sp.	•	5C	
Caheniasaccites ovatus (Bose & Kar 1966) Gutiérrez 1993	r	7B, C	
Caheniasaccites sp.	r	6G, H	*
Cannanoropollis janakii Potonié & Sah 1960	u	5G, H	*
Cannanoropollis mehtae (Lele 1964) Bose & Maheshwari 1968	r	5D, E	*
Cannanoropollis perfectus (Bose & Maheshwari 1968) Dias-Fabrício 1981	•	5F	
Cannanoropollis sp.	•	5O	
Cycadopites cymbatus (Balme & Hennelly 1956) Hart 1965	c	8E–H	* ✓
Cycadopites sp.	•	8I	
Limitisporites rectus Leschik 1956	u	6K–N	* ✓
Limitisporites sp. 1	r	6N, O	
Limitisporites sp. 2	r	7A	
Marsupipollenites striatus (Balme & Hennelly 1956) Hart 1965	•	8B	* ✓
cf. *Marsupipollenites striatus* (Balme & Hennelly 1956) Hart 1965	r	8C/D	
Plicatipollenites densus Srivastava 1970	r	5I	
Plicatipollenites gondwanensis (Balme & Hennelly 1956) Lele 1964	r	5J	*
Plicatipollenites malabarensis (Potonié & Sah 1960) Foster 1975	r	5K, L	*
Plicatipollenites sp. cf. *P. triangularis* Lele 1964	•	5M	
Plicatipollenites sp.	r	5N	
Potonieisporites brasiliensis (Nahuys, Alpern & Ybert 1968) emend. Archangelsky & Gamerro 1979	r	6F	
Potonieisporites novicus Bhardwaj 1954	u	6A–C	✓

Potonieisporites sp. cf. *P. methoris* (Hart 1960) Foster 1975	r	6I, J	
Potonieisporites sp.	•	6D, E	
Protohaploxypinus amplus (Balme & Hennelly 1955) Hart 1964	u	7H	✓
Protohaploxypinus goraiensis (Potonié & Lele 1961) Hart 1964	u	7G, K	
Protohaploxypinus limpidus (Balme & Hennelly 1955) Balme & Playford 1967	u	7P, Q	* ✓
Pteruchipollenites gracilis (Segroves 1969) Foster 1979	r	7D	* ✓
Pteruchipollenites sp. cf. *P. gracilis* (Segroves 1969) Foster 1979	r	7E	
Striatoabieites multistriatus (Balme & Hennelly 1955) Hart 1964	u	7L–N/O	* ✓
Striatopodocarpites sp. 1	•	7I	
Striatopodocarpites sp. 2	•	7J	
Triadispora sp. 1	•	5Q	
Triadispora sp. 2	r	5R, S	
Vittatina fasciolata (Balme & Hennelly 1956) Bharadwaj 1962	r	7R, S	
Vittatina scutata (Balme & Hennelly 1956) Bharadwaj 1962	u	7T–V	✓
Algal microfossils			
Cymatiosphaera sp. cf. *C. gondwanensis* (Tiwari 1965) Backhouse 1991	r	9E/F	
Leiosphaeridia sp.	r	9A	
Maculatasporites sp. cf. *M. indicus* Tiwari 1964	r	9D	
Maculatasporites sp. 1	r	9G	
Maculatasporites sp. 2	r	9H	
Quadrisporites horridus Hennelly 1958 emend. Potonié & Lele 1961	r	9I	* ✓
Spongocystia eraduica Segroves 1967	r	9B/C	* ✓
Tetraporina sp.	u	8J–M	
Foraminifera			
Microforaminiferal test linings	r	9L, M	
Disarticulated polychaete annelid jaws			
Scolecodonts	•	9J, K	

a – abundant (>15%); c – common (>5 – 15%); u – uncommon (1–5%); r – rare (<1%); • – present, but not in count traverse.

* reported by Foster (in Foster *et al.* 1985, fig. 3, column 1; sample WA17).

✓ reported by Backhouse (1993, fig. 9).

All 109 figured specimens are preserved in strew slides housed permanently in the Paleontological Type Collection maintained by the Geological Survey of Western Australia, 37 Harris Street, Carlisle, Western Australia 6101. Curatorial information is provided in Appendix 1.

COMPOSITION OF PALYNOFLORA

The spore component comprises 17 genera (15 trilete, 2 monolete) and pollen grains comprise 15 genera (3 bisaccate non-taeniate, 3 bisaccate taeniate, 6 monosaccate, and one each of monocolpate, praecolpate, and polyplicate genera). Algal palynomorphs are represented by six genera and polychaete annelids by infrequent, unnamed scolecodonts (Table 1).

Land-derived spores and pollen grains dominate this characteristically Eastern Gondwanan Permian palynoflora, both quantitatively and qualitatively (Table 1), and are accompanied by sparse representation of aquatic algal palynomorphs, and rare scolecodonts and microforaminiferal test linings (aka palynoforaminifera: Arai & Koutsoukos 1998). The most common spores are *Leiotriletes directus* Balme & Hennelly 1956, *Densoisporites solidus* Segroves 1970 and *Brevitriletes cornutus* (Balme & Hennelly 1956) Backhouse 1991. Pollen species are diversely, if somewhat less commonly represented; the monocolpate *Cycadopites cymbatus* (Balme & Hennelly 1956) Hart 1965 is the most frequently encountered species. Of the palynoflora's minor but clearly autochthonous or near-autochthonous elements, an unnamed species of *Tetraporina* Naumova 1939 emend. Lindgren 1980 is the most common.

TAXONOMIC COMMENTARY

Aptly and aphoristically termed 'the backbone of palynology' (Gravendyck *et al.* 2021), taxonomy is the prime basis for establishing a practical and reliable spore-pollen stratigraphic zonation. As essential prerequisites, taxa selected to define a particular palynozone should have morphological integrity (as represented foremost

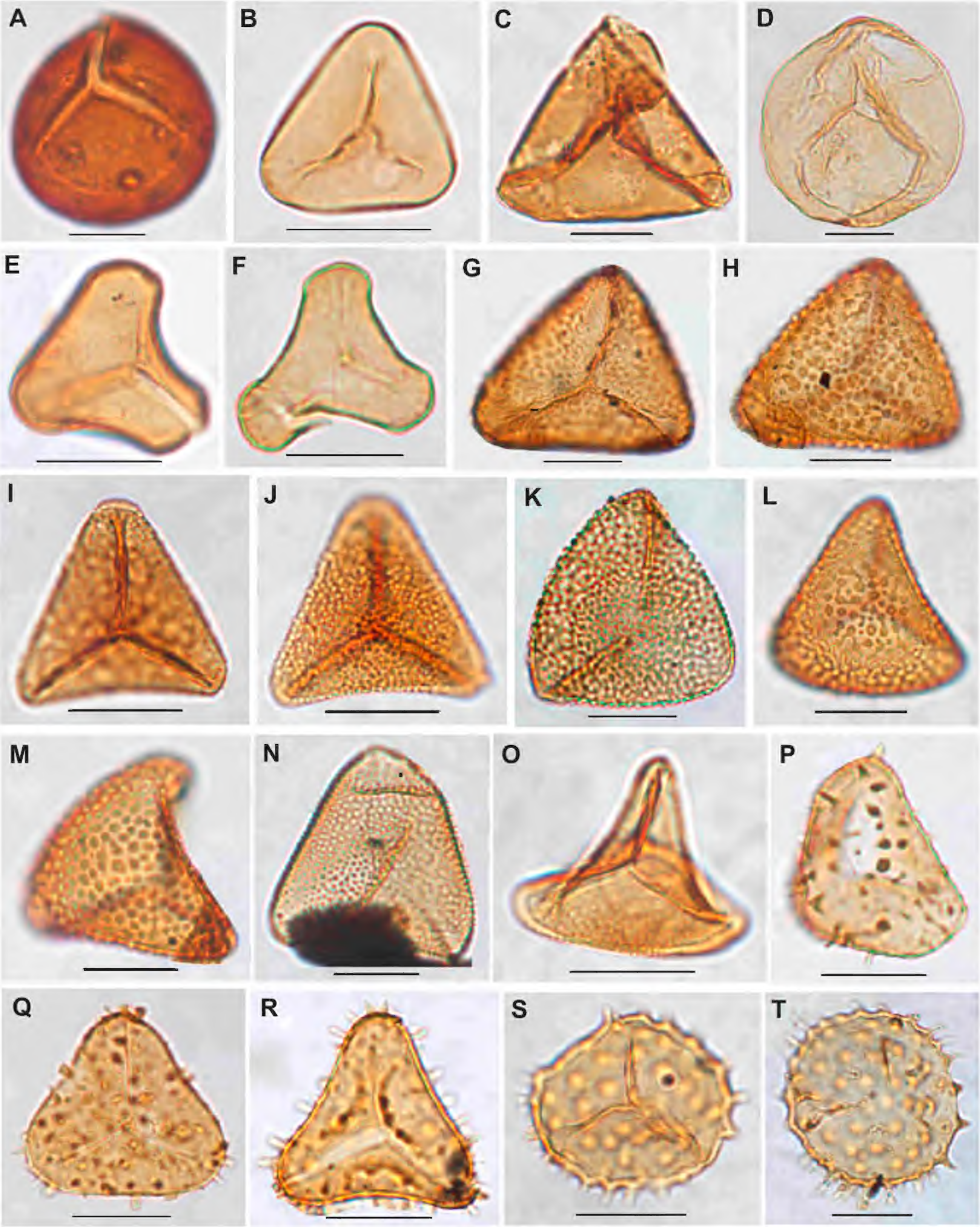

Figure 3. A, *Punctatisporites gretensis*, proximal focus. B, *Leiotriletes directus*, medial focus. C, *Leiotriletes badamensis*, proximal focus. D, *Calamospora* sp., proximal focus. E, F, *Waltzispora* sp., medial and proximal foci. G/H, *Converrucosisporites micronodosus*, proximal/distal foci. I/J–L, *Converrucosisporites confluens*, proximal/distal foci, distal foci. M, *Converrucosisporites naumoviae*, distal focus. N, *Granulatisporites austroamericanus*, distal focus. O, *Microbaculispora tentula*, proximal focus. P, *Horriditriletes curvibaculosus*, distal focus. Q, R, *Horriditriletes ramosus*, proximal foci. S–T, *Brevitriletes cornutus*, proximal and medial foci. Scale bars = 20 μm. See Appendix 1 for curatorial details.

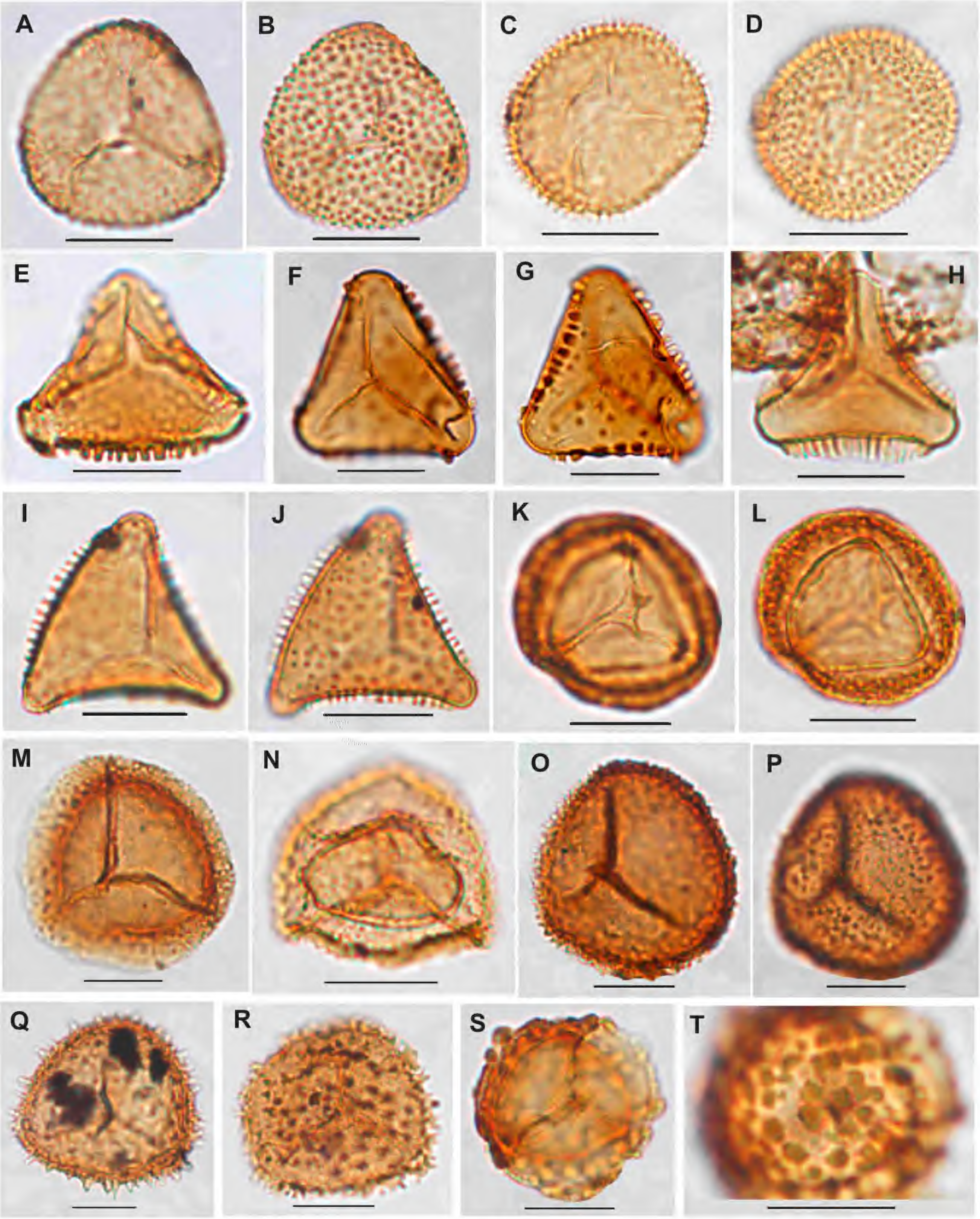

Figure 4. A/B, *Apiculiretusispora* sp. 1, proximal/distal foci. C/D, *Apiculiretusispora* sp. 2, proximal/distal foci. E, F/G, *Diatomozonotriletes townrowii*, near-proximal focus and proximal/medial foci. H, *Diatomozonotriletes* sp. cf. *D. saetosus*, medial focus. I/J, *Diatomozonotriletes* sp., proximal/medial foci. K/L, *Densoisporites solidus*, proximal/medial foci. M, *Indotriradites niger*, proximal focus. N, *Gondisporites bharadwajii*, medial focus. O/P, *Gondisporites wilsonii*, proximal/distal foci. Q, R, *Gondisporites ewingtonensis*, medial and distal foci. S/T, *Secarisporites lacunatus*, proximal/distal foci. Scale bars = 20 μm. See Appendix 1 for curatorial details.

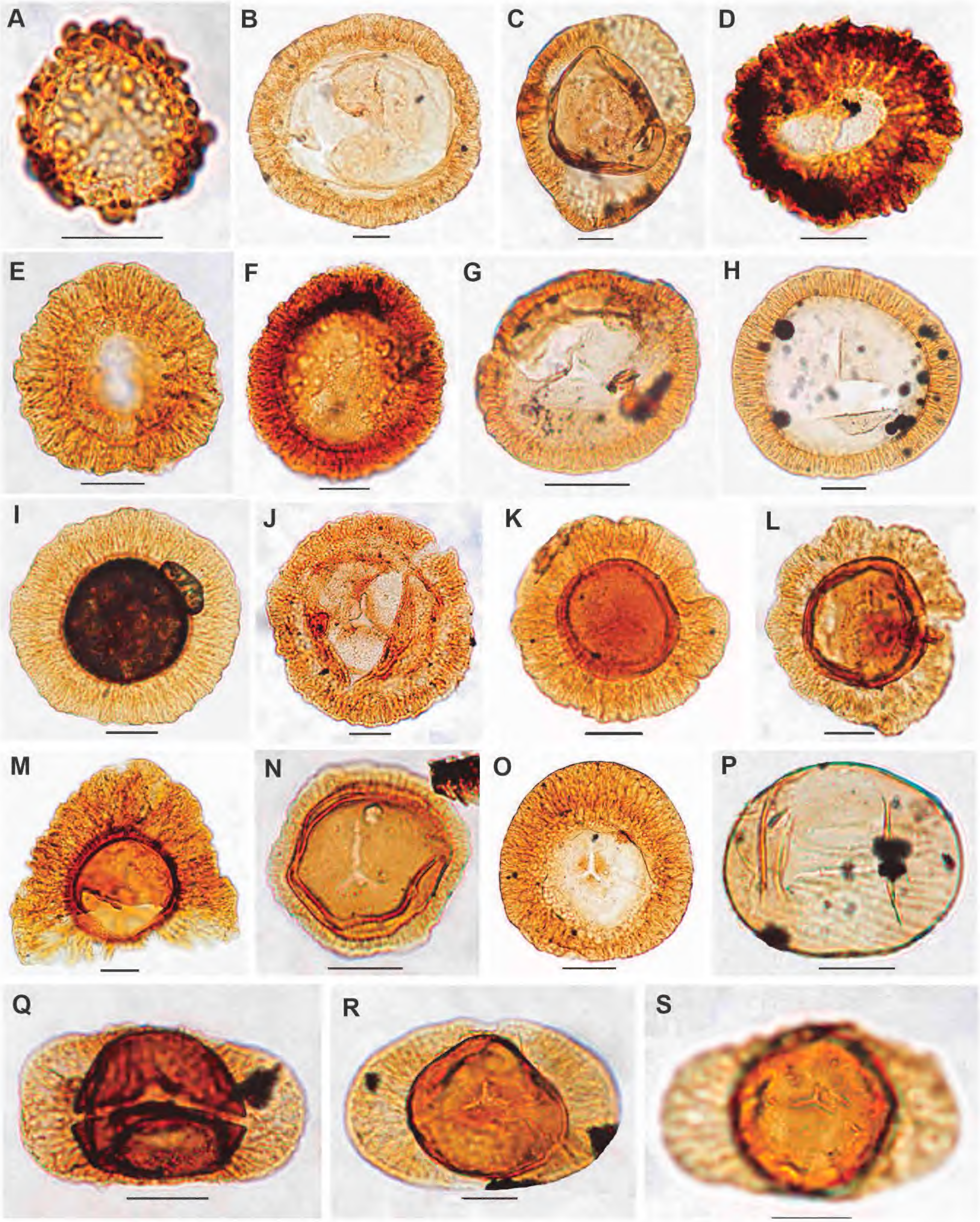

Figure 5. A, *Secarisporites lacunatus*, medial focus. B, *Barakarites rotatus*, medial focus. C, *Barakarites* sp., medial focus. D, E, *Cannanoropollis mehtae*, medial foci. F, *Cannanoropollis perfectus*, proximal focus. G, H, *Cannanoropollis janakii*, proximal foci. I, *Plicatipollenites densus*, medial focus. J, *Plicatipollenites gondwanensis*, proximal focus. K, L, *Plicatipollenites malabarensis*, proximal foci. M, *Plicatipollenites* sp. cf. *P. triangularis*, medial focus. N, *Plicatipollenites* sp., proximal focus. O, *Cannanoropollis* sp., proximal focus. P, *Kendosporites striatus*, medial focus. Q, *Triadispora* sp. 1, medial focus. R, S, *Triadispora* sp. 2, proximal foci. Scale bars = 20 µm, except O (= 50 µm). See Appendix 1 for curatorial details.

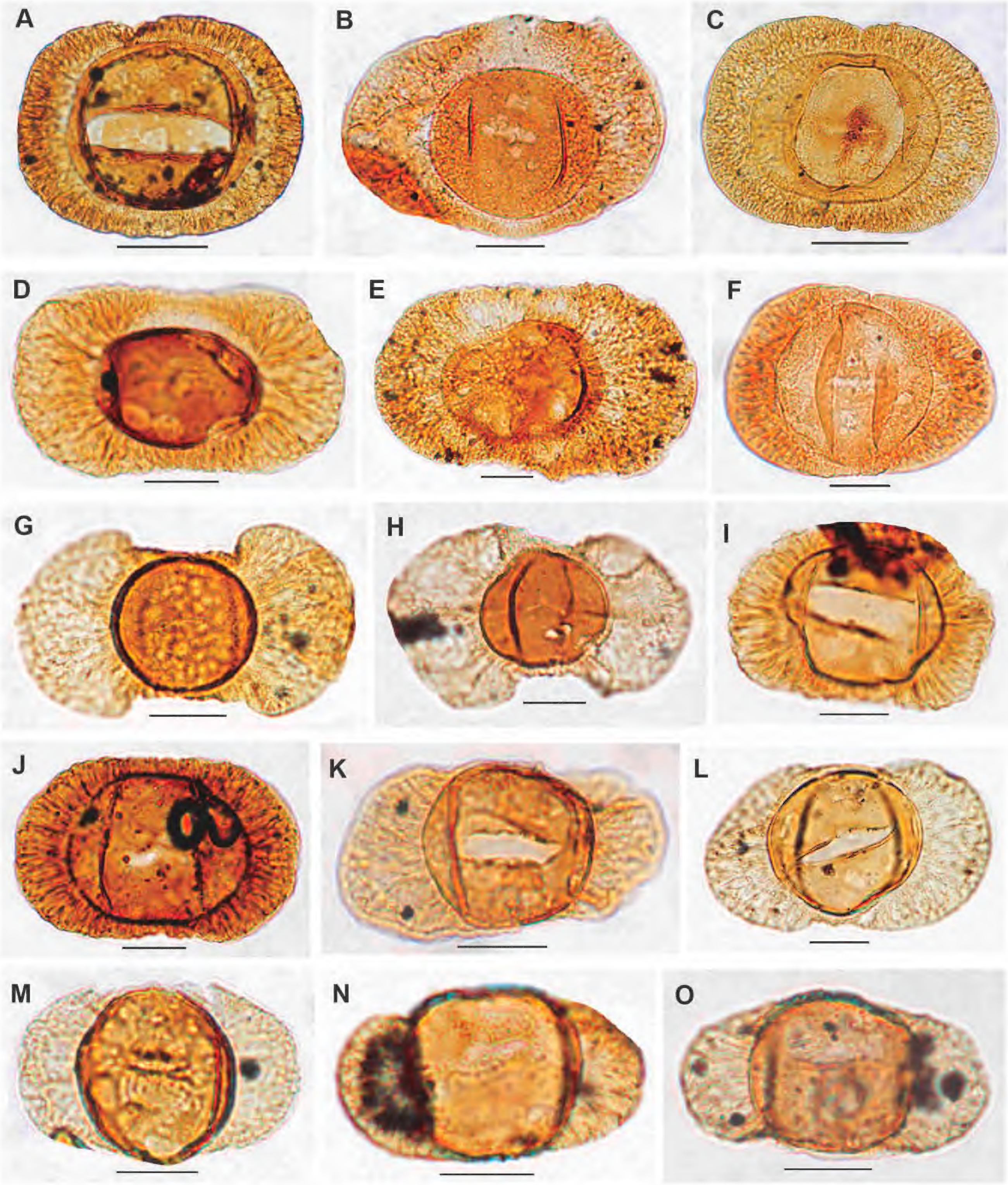

Figure 6. A–C, *Potonieisporites novicus*, medial foci. D, E, *Potonieisporites* sp., medial foci. F, *Potonieisporites brasiliensis*, proximal focus. G, H, *Caheniasaccites* sp., medial and proximal foci. I, J, *Potonieisporites* sp. cf. *P. methoris*, proximal and medial foci. K–M, *Limitisporites rectus*, proximal foci (K, L), medial focus (M). N, O, *Limitisporites* sp. 1, medial foci. Scale bars = 20 μm, except A (= 50 μm). See Appendix 1 for curatorial details.

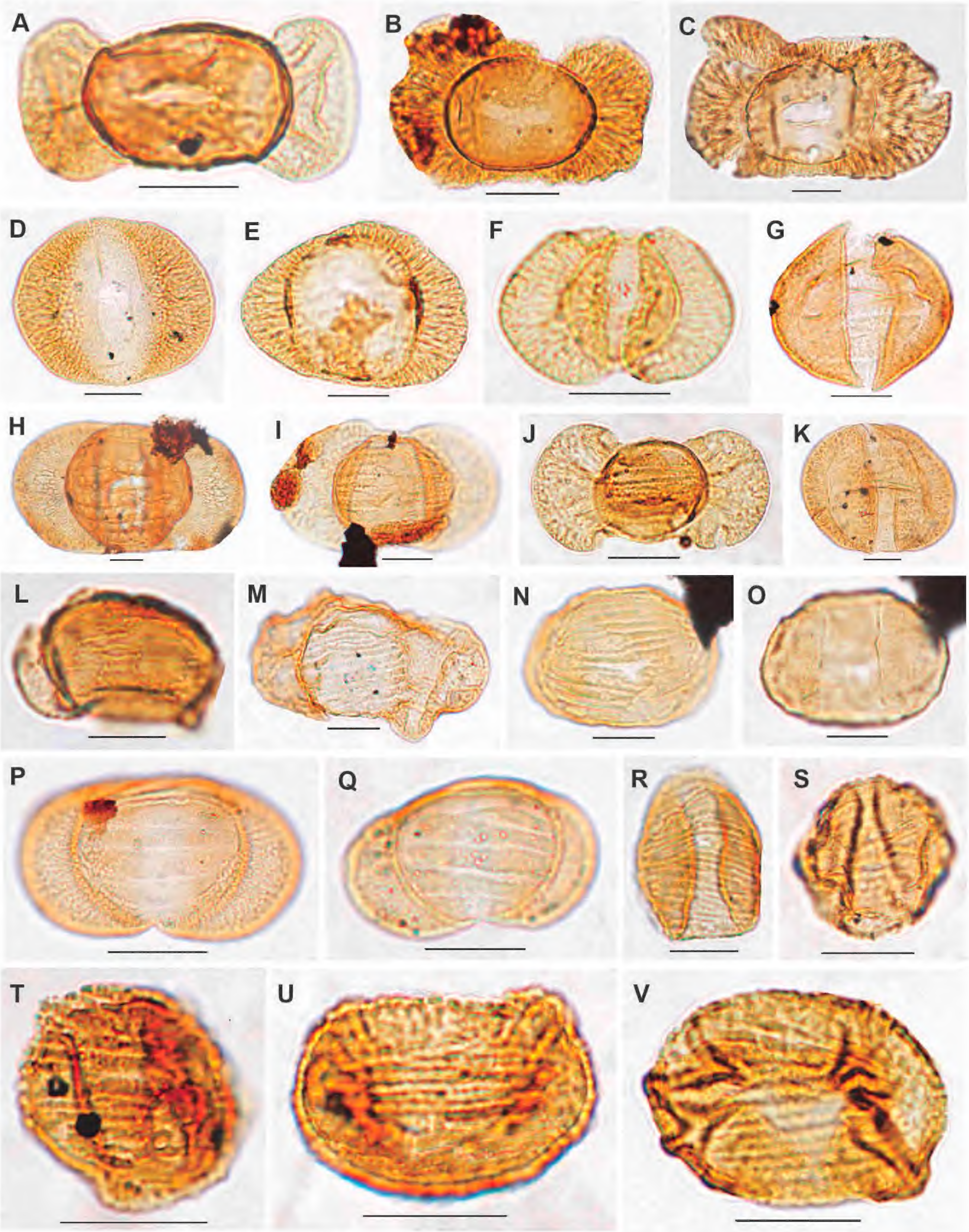

Figure 7. A, *Limitisporites* sp. 2, medial focus. B, C, *Caheniasaccites ovatus*, medial and proximal foci. D, *Pteruchipollenites gracilis*, medial focus. E, *Pteruchipollenites* sp. cf. *P. gracilis*, medial focus. F, *Alisporites* sp., distal focus. G, K, *Protohaploxypinus goraiensis*, medial foci. H, *Protohaploxypinus amplus*, proximal focus. I, *Striatopodocarpites* sp. 1, near-proximal focus. J, *Striatopodocarpites* sp. 2, medial focus. L–N/O, *Striatoabieites multistriatus*, proximal foci (L, M), proximal/distal foci (N/O). P, Q, *Protohaploxypinus limpidus*, medial and proximal foci. R, S, *Vittatina fasciolata*, medial foci. T–V, *Vittatina scutata*, medial foci. Scale bars = 20 μm. See Appendix 1 for curatorial details.

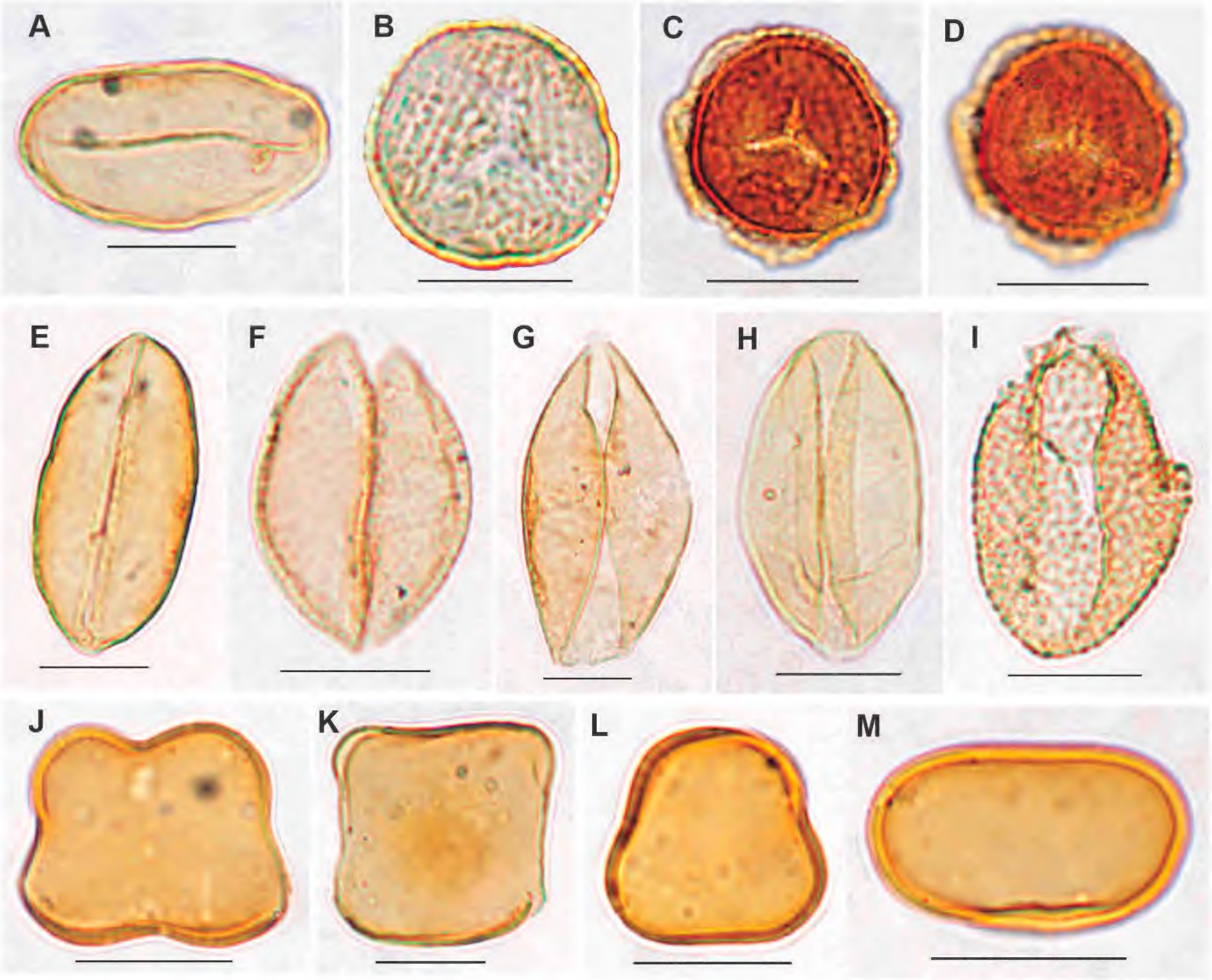

Figure 8. A, *Laevigatosporites* sp., medial focus. B, *Marsupipollenites striatus*, medial focus. C/D, cf. *Marsupipollenites striatus*, proximal/distal foci. E–H, *Cycadopites cymbatus*, medial foci. I, *Cycadopites* sp., medial focus. J–M, *Tetraporina* sp., medial foci. Scale bars = 20 µm. See Appendix 1 for curatorial details.

by their published type material), together with well-defined stratigraphic ranges (first- and/or last-appearance datums) or, less commonly and less definitively, prominent and consistent quantitative acmes or minima.

With many refinements in preparatory techniques, microscopy and photomicrography over the last half-century or so, it is inevitable that some palynomorph species instituted decades ago are difficult to identify with certainty or to be clearly differentiable from other morphologically similar species. This especially applies when the palynoflora being studied, as here, is much better preserved than in many relevant prior publications. Some taxonomic uncertainties encountered during the present study are discussed below and their future resolution would facilitate improved palynostratigraphic precision. No attempt was made at systematic identifications of the few, mostly in situ scolecodonts in view of the taxonomic instability associated with these largely disarticulated polychaete jaw apparatuses.

The zonal eponym *Converrucosisporites confluens* (Archangelsky & Gamerro 1979) Playford & Dino 2002 (p. 246, 248; pl. 2, figs 3–8) has, since its institution >40 years ago, become a confused or 'balloon' taxon, with some putative identifications straying appreciably beyond Archangelsky & Gamerro's (1979, p. 422–423, pl. I, figs 5, 6) original definition based on Argentine material (e.g. Césari *et al*. 1995, pl. 1, fig. 12). Cognizant of this taxonomic dilemma, Césari *et al*. (2013) pointed to the possibility or likelihood of morphological intergradation linking *C. confluens* with such species as *Granulatisporites austroamericanus* Archangelsky & Gamerro 1979 and *Converrucosisporites micronodosus* (Balme & Hennelly 1956) Playford & Dino 2002. Moreover, Playford & Dino (2002), inter alia, have alluded to the possibility that *G. austroamericanus* and *Microbaculispora tentula* Tiwari 1965 are conspecific. However, each of these three species is recorded discretely herein pending provision of more definitive information on the latter's type material (Tiwari 1965, p. 175–176; pl. 2, figs 35–37; text-fig. 2e). Backhouse & Mory (2020, p. 51) commented that *C. confluens* is with 'little doubt … a morphologic development from *M. tentula*.' Resolution of this taxonomic conundrum is outside the scope of the present account; however, it is relevant to point out that:

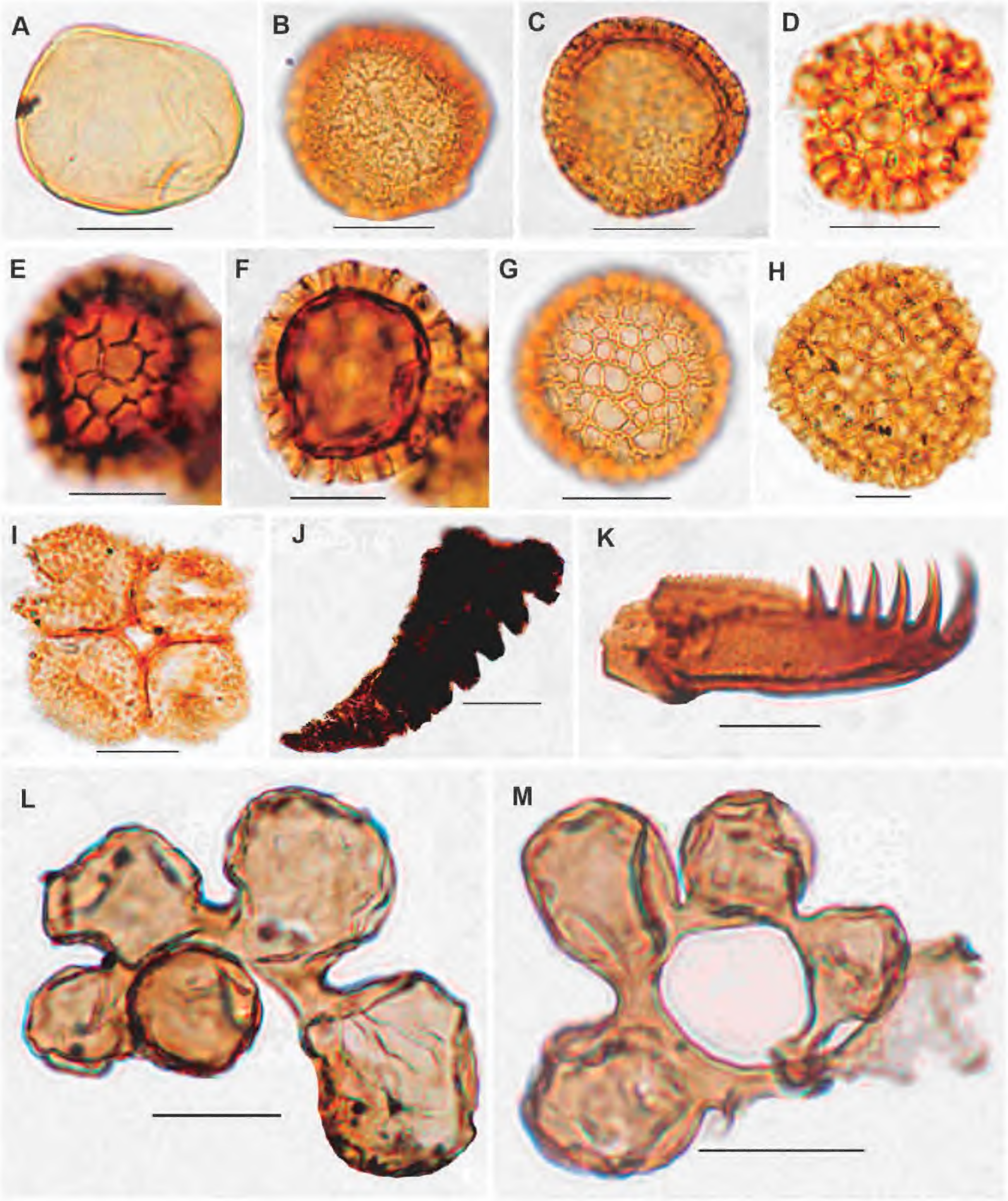

Figure 9. A, *Leiosphaeridia* sp., medial focus. B/C, *Spongocystia eraduica*, high/medial foci. D, *Maculatasporites* sp. cf. *M. indicus*, low focus. E/F, *Cymatiosphaera* sp. cf. *C. gondwanensis*, high/medial foci. G, *Maculatasporites* sp. 1, high focus. H, *Maculatasporites* sp. 2, medial focus. I, *Quadrisporites horridus*, medial focus. J, K, scolecodonts. L, M, microforaminiferal test linings. Scale bars = 20 μm. See Appendix 1 for curatorial details.

(a) Australian identifications of *Converrucosisporites confluens* by Backhouse (1991, pl. VI, figs 1–4) and Foster (in Foster & Waterhouse 1988, fig. 5f, i; albeit doubtfully fig. 4a–c) are consonant with Archangelsky & Gamerro's (1979) species diagnosis, as are those recorded herein (Fig. 3I/J–L) and by, inter alia, Vergel (1998) and Playford & Dino (2002, from Argentina) Stephenson (1998, from Oman), Stephenson (2009, from Namibia) and Kavali *et al*. (2021, from India). These and other reports connote the widespread dissemination of *C. confluens* through Eastern, Western and Northern Gondwana during the Cisuralian.

(b) *Pseudoreticulispora pseudoreticulata* (Balme & Hennelly 1956) Bharadwaj & Salujha 1969 (not recorded in the Woolaga assemblage) is distinguishable from *C. confluens* à propos of its mainly larger size and coarser sculpture (e.g. Price 1983, pl. 5, figs 1–9; Backhouse 1991, pl. VI, figs 1–4 vs. figs 5–9; Stephenson & McLean 1999, fig. 4a, b). Backhouse & Mory (2020, p. 14) cautioned that, in some reports, *C. confluens* has been misidentified as *P. pseuedoreticulata*, with ensuing doubtful or incorrect palynozonal assignments.

Two trilete apiculate species—*Horriditriletes tereteangulatus* (Balme & Hennelly 1956) Backhouse 1991 and *H. ramosus* (Balme & Hennelly 1956) Backhouse 1991 (the latter recorded herein)—have been differently interpreted, and variously reported, by later authors (e.g. Rigby & Hekel 1977). This is chiefly because the diagnoses and photomicrographs furnished by the original authors (Balme & Hennelly 1956b, p. 247, pl. 2, figs 27–29 and p. 249, pl. 3, figs 39–41, respectively) are insufficiently definitive for the two species to be recognized conclusively and individually. In the present account, identification of *H. ramosus*, as distinct from *H. tereteangulatus*, accords with Foster (1979, p. 39, pl. 7, figs 9–12), Playford & Rigby (2008, p. 18–19, pl. 3, figs 1, 2) and Backhouse (1991, pl. II, figs 14, 15a, b vs. figs 6–9). This applies likewise to the separate recognition, in the two last-named papers, of *H. filiformis* (Balme & Hennelly 1956b, p. 247, pl. 2, figs 22, 23) Backhouse 1991. Note that a specimen figured by Peyrot *et al.* (2019, fig. 3O) as *H. tereteangulatus* is clearly representative of *H. ramosus*. *Horriditriletes uruguayensis* (Marques-Toigo 1974) Archangelsky & Gamerro 1979 (p. 424–426; pl. II, figs 2–4) differs little from, and could well be synonymous with, *H. ramosus*; see also Kavali *et al*. (2021, fig. 4.14, 4.16).

The stratigraphically important species *Diatomozonotriletes townrowii*, as defined by Segroves (1970, p. 54–55, pl. 3, figs D–G) and recorded herein (Fig. 4E, F/G), has been identified authentically in many reports (e.g. Backhouse 1991; Balme & Backhouse 1993; Stephenson & McLean 1999; Backhouse & Mory 2020). However, Rigby & Hekel's (1977, p. 9, pl. 2, figs 7, 8) comparative (cf.) identification of *D. townrowii* from the Permian of central Queensland differs conspicuously from the species as originally defined, not simply 'only in having shorter laesurae.' Foster in Foster *et al.* (1985) suggested assignment of those specimens to *Interradispora* Price 1979.

Most of the pollen grains could be identified at specific level with reasonable confidence. However, some uncertainties arise at generic level. For instance, the distinction between *Cannanoropollis* Potonié & Sah 1960 and *Plicatipollenites* Lele 1964 is not always clear cut; and the same evidently applies for *Alisporites* Daugherty 1941 and *Pteruchipollenites* Couper 1958. The recent affirmation (di Pasquo *et al*. 2021) that *Faunipollenites* Bharadwaj 1962 and *Protohaploxypinus* Samoilovich 1953 emend. Morbey 1975 are congeneric confirms the present assignments to the latter of the three species recorded herein.

The pollen grains here identified as cf. *Marsupipollenites striatus* (Balme & Hennelly 1956) Hart 1965 (Fig. 8C/D) are morphologically close to those reported as Balme & Hennelly's (1956a, p. 61, pl. 2, figs 36, 37) species by Foster (1979) and Backhouse (1991), but differ in possessing a relatively narrow equatorial zone. This disparity could possibly be a consequence of more complete preservation seen in the Woolaga Limestone material. Additionally, a single specimen encountered in the present study (Fig. 8B) is identified as *M. striatus*.

Two monosulcate species—*Vittatina fasciolata* (Balme & Hennelly 1956a, p. 62, pl. pl. 3, figs 42–45) Bharadwaj 1962 and *V. sulcata* (Balme & Hennelly 1956a, p. 62, pl. 3, figs 38–41) Bharadwaj 1962—are similar morphologically and thus prone to be differentiated on somewhat nuanced criteria by different authors (e.g. Rigby & Hekel 1977; Backhouse 1991; Balme & Backhouse 1993). The identifications herein (Figs 7R, S and T–V, respectively) are essentially consonant with the two last-cited publications.

The relatively common, inaperturate specimens of the algal genus *Tetraporina*, as reported here, form a morphological, non-speciated near-continuum, with outline varying among square, rectangular, subcircular and elliptical (Fig. 8J–M; see also Segroves 1967, pl. 3, fig. 22; Foster in Foster *et al*. 1985, pl. 1, figs 16, 22). Of the representatives of the genus *Maculatasporites* Tiwari 1964 recorded herein, that labelled informally as *M*. sp. 1 (Fig. 9G) appears similar to pollen of *Tribulus terrestris* Linné 1753 of the angiosperm family Zygophyllaceae (Sanchez Botero 2021, pl. 1, fig. 12). However, in detail (Nasri-Ayachi & Nabli 2009), the resemblance is superficial.

PALYNOSTRATIGRAPHIC CORRELATION AND DATING

Systematic documentation of palynomorphs from the Perth Basin's Permian strata—inaugurated in a series of publications (Balme & Segroves 1966; Segroves 1967, 1969, 1970)—was based on samples from boreholes distributed through the basin's northern sector, including the Woolaga Creek area (Segroves 1970, figs 1–3). Stratigraphic ranges of the spores and non-saccate pollen grains within the Permian succession were charted initially by Segroves (1970, fig. 4) and subsequently, and taxonomically more comprehensively, by Segroves (1972, fig. 4). In the latter paper, four stratigraphically successive palynological assemblages were proposed. Of these, the *Quadrisporites* Assemblage was shown as occupying the bulk of the Holmwood Shale including the uppermost Fossil Cliff Member, then known as a separate formation (Segroves 1972, p. 514; figs 1, 4; pls II, III). Not unexpectedly, the samples of the present study are generally compatible with the *Quadrisporites* Assemblage. Foster (in Foster *et al.* 1985) reported an abundant and varied palynoflora from a sample collected from the type section of the Fossil Cliff Member in the Irwin River area. Mirroring to some extent the case with the Woolaga Limestone samples of the present study, Foster expressed surprise that his outcrop sample proved palyniferous. As indicated in Table 1, a large number of the species listed in Foster *et al*. (1985, fig. 3) are common to the Woolaga Limestone palynoflora.

The vertical ranges of certain species recorded herein were modified or instituted by later studies of Western Australian Permian palynofloras, most notably by John Backhouse; viz. Backhouse (1988, 1991) for the Collie Basin; Backhouse (1993), Perth, Collie and Officer basins; Backhouse (1998), all basins; Mory & Backhouse (1997), Carnarvon Basin; and Backhouse & Mory (2020), Canning Basin. Backhouse (1991, fig. 10) established a palynostratigraphic (spore-pollen) zonal scheme designed to be applicable to Permian successions of Western Australian basins. In particular, Backhouse (1991, fig. 11) provided a comprehensive chart detailing the vertical ranges of palynomorph species, characterized zonally, through Permian strata of the Collie Basin. Subsequently, and of particular relevance here, Backhouse (1993, p. 118–120, fig. 9) documented the vertical distribution of species in the Nangetty Formation and overlying Holmwood Shale in the northern Perth Basin. The palyniferous samples were from six named boreholes in the Irwin River and Woolaga Creek areas, with depth intervals juxtaposed successively (Backhouse 1993, figs 4, 9) and embracing, in ascending order, the following palynostratigraphic units: Stage 2, *Pseudoreticulatispora confluens* (reassigned to *Converrucosisporites*) and *Pseudoreticulatispora pseudoreticulata*.

Twenty-one of the species documented by Backhouse (1993, fig. 9) are positively identified in the present material, including the following considered of particular stratigraphic relevance: *Converrucosisporites confluens, Densoisporites solidus, Diatomozonotriletes townrowii, Potonieisporites novicus* Bhardwaj 1954, *Spongocystia eraduica* Segroves 1967, *Striatoabieites multistriatus* (Balme & Hennelly 1955) Hart 1964 and *Vittatina scutata*. Collectively, these species would suggest assignment of the Woolaga Limestone Member to either the *C. confluens* Zone or the *P. pseudoreticulata* Zone. The presence of *Diatomozonotriletes*—*D. townrowii* in particular, cited by Backhouse & Mory 2020 (p. 60) as 'an index species for the base of the *P. pseudoreticulata* Zone'—would tend to favour the second option, notwithstanding the seeming absence of the eponymous *P. pseudoreticulata*. Alternatively, *C. confluens* would suggest the first option. Thus the Woolaga Limestone Member's palynoflora, as hosted by the two study samples, is here considered assignable to either the *P. pseudoreticulata* Zone or the upper or uppermost *C. confluens* Zone. The Fossil Cliff Member in the Irwin River area, containing both *D. townrowii* and *P. pseudoreticulata* (Foster in Foster *et al*. 1985), is obviously representative of the *P. pseudoreticulata* Zone.

In 1976, Kemp *et al*. discussed uncertainties in the age-dating of many Australian Carboniferous–Permian palynostratigraphic units and the situation has not changed appreciably since then. However, as noted previously, the Woolaga Limestone Member's ammonoid content in particular is regarded as indicative of a Sakmarian age, which is moreover considered applicable to the bulk of the Holmwood Shale (e.g. Mory *et al*. 2005; Mory & Haig 2011; Haig *et a*l. 2014); this provides a useful age constraint to the palynological content.

However, more recently Backhouse & Mory (2020, p. 14, figs 3, 5) proposed an Asselian age for the Holmwood Shale, and its constituent *C. confluens* and lower *P. pseudoreticulata* spore-pollen zones. They stated that 'Volcanic ash beds identified by Gorter *et al.* (2005) from the Ditji Formation in the Bonaparte Basin have yielded preliminary zircon dates of about 295 Ma, i.e. within the Asselian, for the *P. confluens – P. pseudoreticulata* Zone boundary.' However, in evaluating that statement, the following should be taken into account:

(a) The above reference to Gorter *et al*. (2005), which dealt exclusively with Carboniferous stratigraphy of the Petrel Sub-basin, was incorrect, the relevant paper being Gorter *et al*. (2008)[1].

(b) The palynozonal attributions, and putative correlation with the Holmwood Shale, should be viewed reservedly insofar as any detail concerning the palynological contents of the Ditji Formation or equivalent strata in the basin are apparently unavailable, at least publicly[2].

(c) The absolute-age determination, of 293±3 Ma (Bradshaw *et al*. 1990; Gorter *et al*. 2008), did not derive from the Ditji Formation. It was based on a 1984 K–Ar analysis of 'a dolerite dyke [the so-called Kulka Dolerite] intersected [within a presumed Permian section] 15 m below the Mesozoic unconformity' in Kulka-1 (Bradshaw *et al*. 1990, p. 117) drilled in the Goulburn Graben of the Arafura Basin. Nevertheless, these data were extrapolated by Gorter *et al*. (2008, p. 102) as applicable to a 'high gamma ray interval in the Ditji Formation interpreted to be an ash fall.'

Although Backhouse & Mory (2020, p. 38) alluded to 'preliminary dates from the Bonaparte [Basin]' indicative of late Asselian cessation of glacial influence in Western Australia, there appear to be no substantive grounds for endorsing an Asselian dating of the Holmwood Shale, which is here reaffirmed as Sakmarian.

PALAEOENVIRONMENTAL SIGNIFICANCE

The predominant spore and pollen components of the palynoflora, and their excellent preservation, indicate substantial input from a range of terrestrial vascular vegetation that evidently flourished near the marine depositional site. Parental sources were spore-producing plants (pteridophytes: sphenophytes, lycophytes, ferns) and the polleniferous gymnosperms (particularly members of the *Glossopteris* Flora); e.g. Rigby (1993), McLoughlin (1993), Balme (1995), Peyrot *et al*. (2019) and McLoughlin & Prevec (2021).

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[1] Editor's comment: The omission in Backhouse & Mory (2020) has been corrected. The revised version can be downloaded from DMIRS eBookshop via www.dmirs.wa.gov.au.

[2] Editor's comment: These open-file reports can be downloaded from the DMIRS WAPIMS database, but typically lack taxonomic discussions or illustrations.

The algal (green-algal) elements—qualitatively and quantitatively much subordinate to the spore-pollen component (Table 1)—are assuredly aquatic. Of these, *Maculatasporites* spp., *Quadrisporites horridus* Hennelly 1958 emend. Potonié & Lele 1961, *Spongocystia eraduica* and *Tetraporina* sp. are regarded as essentially non-marine (freshwater or brackish), whereas *Leiosphaeridia* sp. and *Cymatiosphaera gondwanensis* (Tiwari 1965) Backhouse 1991 could be either marine or non-marine (Brenner & Foster 1994; Grenfell 1995; Mays *et al*. 2021). The few scolecodonts and microformaminiferal test linings signify a normal marine environment. However, one of the figured scolecodonts (Fig. 7J), which is less well preserved and much darker than the other (Fig. 7K), could well be remanié. Given the marine depositional environment of the Woolaga Limestone Member, its palynoflora contains both allochthonous (spores and pollen grains) and autochthonous or near-autochthonous (other groups) components.

CONCLUSIONS

(1) Because surface exposures of Australian sedimentary rocks are normally devoid of palynological microfossils due to intensive Cenozoic weathering, the diverse and well-preserved palynoflora from the Woolaga Limestone Member is highly unusual. This has likely resulted from being protected from oxidative desiccation, and flattening by overburden pressure, by early calcareous cementation.

(2) The palynoflora—overwhelmingly dominated, quantitatively and qualitatively, by terrestrial spores and pollen grains—testifies to prolific pteridophytes and gymnosperms (notably glossopterids) flourishing close to the marine depositional site, and with essentially minor contributions from in situ, or close to in situ, green algae, microforaminifers and polychaete annelids completing the palyno-biocenosis.

(3) In palynostratigraphic terms, the spore-pollen component, characteristically early Permian in composition, is referable to either the *Converrucosisporites confluens* Zone or the succeeding *Pseudoreticulatispora pseudoreticulata* Zone as currently recognized in Western Australian Permian strata.

(4) The potential for *C. confluens* and *P. pseudoreticulata* to be confused is unfortunate given their current status as eponymous indices of successive palynozones.

(5) Notwithstanding a recent suggestion of an earlier Permian (Asselian) age for the *C. confluens* Zone and lower *P. pseudoreticulata* Zone (lower part), a Sakmarian age, as signified primarily by the ammonoid fauna, is here reaffirmed for the Woolaga Limestone Member.

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APPENDIX 1

Inventory of palynomorphs illustrated in Figures 3–9. Precise locations of individual specimens on numbered slides are specified by EF coordinates secured via a standard England Finder™ gridded slide. Specimen catalogue numbers (GSWA F55040–F55147, F55165) are those of the permanent repository: Geological Survey of Western Australia, Paleontological Type Collection, 37 Harris Street, Carlisle, WA 6101, Australia.

Palynomorphs	Figure no.	Sample no.	Slide no.	EF coords	Photo no.	GSWA no.
Punctatisporites gretensis	3A	175035	1	P19/1	WL09	F55040
Leiotriletes directus	3B	175035	3	P23	WL684	F55041
Leiotriletes badamensis	3C	175035	3	X36/2	WL1005	F55042
Calamospora sp.	3D	175035	3	R34/1	WL750	F55043
Waltzispora sp.	3E	175035	1	J20/4	WL13	F55044
Waltzispora sp.	3F	175035	3	J41/4	WL823	F55045
Converrucosisp. micronodosus	3G/H	175029	5	D24/3	WL947/48	F55046
Converrucosisp. confluens	3I/J	175035	2	W30/1	WL447/48	F55047
Converrucosisp. confluens	3K	175035	12	G11/3	WL1150	F55048
Converrucosisp. confluens	3L	175035	3	K41	WL824	F55049
Converrucosisp. naumoviae	3M	175035	3	N34/4	WL755	F55050
Granulatisp. austroamericanus	3N	175035	3	K45	WL876	F55051
Microbaculispora tentula	3O	175035	3	K49	WL908	F55052
Horriditriletes curvibaculosus	3P	175035	2	U17	WL338	F55053
Horriditriletes ramosus	3Q	175035	3	R36	WL768	F55054
Horriditriletes ramosus	3R	175035	1	S30/3	WL56	F55055
Brevitriletes cornutus	3S	175035	3	K40/1	WL817	F55056
Brevitriletes cornutus	3T	175035	2	D32	WL456	F55057
Apiculiretusispora sp. 1	4A/B	175035	3	L17/1	WL625/26	F55058
Apiculiretusispora sp. 2	4C/D	175035	3	P18/3	WL629/30	F55059
Diatomozonotriletes townrowii	4E	175035	2	O26/1	WL416	F55060
Diatomozonotriletes townrowii	4F/G	175035	3	Q47/3	WL884/86	F55061
Diatomozonotriletes cf. *saetosus*	4H	175035	2	K13	WL264	F55062
Diatomozonotriletes sp.	4I/J	175035	2	N46/2	WL547/48	F55063
Densoisporites solidus	4K/L	175035	3	S21	WL669/70	F55064
Indotriradites niger	4M	175035	3	H17/1	WL615	F55065
Gondisporites bharadwajii	4N	175035	3	S42/4	WL844	F55066
Gondisporites wilsonii	4O/P	175029	14	X22/3	WL1240/41	F55067
Gondisporites ewingtonensis	4Q	175029	4	G27/1	WL913	F55068
Gondisporites ewingtonensis	4R	175029	9	M24/2	WL172	F55069
Secarisporites lacunatus	4S/T	175035	3	J21	WL674/76	F55070
Secarisporites lacunatus	5A	175035	2	H40/4	WL517	F55071
Barakarites rotatus	5B	175029	6	R14/4	WL964	F55072
Barakarites sp.	5C	175029	5	R23/2	WL82	F55073
Cannanoropollis mehtae	5D	175035	1	C35	WL62	F55074
Cannanoropollis mehtae	5E	175029	9	M28/3	WL183	F55075
Cannanoropollis perfectus	5F	175035	1	E19/4	WL11	F55076
Cannanoropollis janakii	5G	175029	5	J19	WL942	F55077
Cannanoropollis janakii	5H	175029	4	E36	WL925	F55078
Plicatipollenites densus	5I	175035	1	N19	WL10	F55079
Plicatipollenites gondwanensis	5J	175029	9	U31/2	WL189	F55080
Plicatipollenites malabarensis	5K	175029	5	M20	WL78	F55081
Plicatipollenites malabarensis	5L	175035	1	E35/1	WL61	F55082
Plicatipollenites cf. *triangularis*	5M	175035	1	T18/1	WL03	F55083
Plicatipollenites sp.	5N	175029	19	W9	WL1356	F55084
Cannanoropollis sp.	5O	175029	8	S30/3	WL138	F55085
Kendosporites striatus	5P	175029	6	S36	WL979	F55086
Triadispora sp. 1	5Q	175035	1	M24/1	WL35	F55087
Triadispora sp. 2	5R	175029	9	R25/2	WL178	F55088
Triadispora sp. 2	5S	175035	2	X22	WL378	F55089
Potonieisporites novicus	6A	175029	17	Q13/2	WL1322	F55090
Potonieisporites novicus	6B	175029	9	G35	WL194	F55091
Potonieisporites novicus	6C	175029	14	D32/2	WL1250	F55092
Potonieisporites sp.	6D	175029	8	L17/4	WL109	F55093

Potonieisporites sp.	6E	175029	8	F12/3	WL104	F55094
Potonieisporites brasiliensis	6F	175029	8	O38/1	WL158	F55095
Caheniasaccites sp.	6G	175035	2	D13	WL262	F55096
Caheniasaccites sp.	6H	175029	6	Q30/3	WL974	F55097
Potonieisporites cf. *methoris*	6I	175035	1	E33/1	WL58	F55098
Potonieisporites cf. *methoris*	6J	175029	8	D32/2	WL145	F55099
Limitisporites rectus	6K	175029	9	R22	WL175	F55100
Limitisporites rectus	6L	175029	5	S18	WL77	F55101
Limitisporites rectus	6M	175035	2	R40	WL507	F55102
Limitisporites sp. 1	6N	175029	9	F21	WL171	F55103
Limitisporites sp. 1	6O	175029	6	D32/1	WL977	F55104
Limitisporites sp. 2	7A	175035	3	P24	WL697	F55105
Caheniasaccites ovatus	7B	175035	2	J23/4	WL387	F55106
Caheniasaccites ovatus	7C	175029	6	T24/3	WL970	F55107
Pteruchipollenites gracilis	7D	175029	8	K24/1	WL125	F55108
Pteruchipollenites cf. *gracilis*	7E	175035	2	C19/3	WL355	F55109
Alisporites sp.	7F	175035	2	W14/4	WL287	F55110
Protohaploxypinus goraiensis	7G	175035	2	K13	WL265	F55111
Protohaploxypinus goraiensis	7K	175029	5	K45/2	WL961	F55112
Protohaploxypinus amplus	7H	175029	9	Q34	WL193	F55113
Striatopodocarpites sp. 1	7I	175035	2	R17	WL341	F55114
Striatopodocarpites sp. 2	7J	175035	2	G29/4	WL728	F55115
Striatoabieites multistriatus	7L	175035	3	D20/1	WL648	F55116
Striatoabieites multistriatus	7M	175029	8	V29	WL137	F55117
Striatoabieites multistriatus	7N/O	175035	3	U37	WL772/73	F55118
Protohaploxypinus limpidus	7P	175035	3	O36/1	WL766	F55119
Protohaploxypinus limpidus	7Q	175035	2	N21/3	WL375	F55120
Vittatina fasciolata	7R	175035	3	K18/3	WL631	F55121
Vittatina fasciolata	7S	175035	3	T30/4	WL732	F55122
Vittatina scutata	7T	175029	8	T31/4	WL141	F55123
Vittatina scutata	7U	175029	9	T27/4	WL179	F55124
Vittatina scutata	7V	175035	2	T41/2	WL524	F55125
Laevigatosporites sp.	8A	175035	2	S48/2	WL567	F55126
Marsupipollenites striatus	8B	175035	10	M20	WL1052	F55127
cf. *Marsupipollenites striatus*	8C/D	175035	3	M37/4	WL784/85	F55128
Cycadopites cymbatus	8E	175035	2	C18/1	WL344	F55129
Cycadopites cymbatus	8F	175035	3	H39	WL808	F55130
Cycadopites cymbatus	8G	175035	2	D15/4	WL325	F55131
Cycadopites cymbatus	8H	175035	3	O42/1	WL838	F55132
Cycadopites sp.	8I	175029	8	J36/1	WL154	F55133
Tetraporina sp.	8J	175035	2	M14	WL277	F55134
Tetraporina sp.	8K	175035	2	N43/3	WL540	F55135
Tetraporina sp.	8L	175035	2	O26/4	WL417	F55136
Tetraporina sp.	8M	175035	3	J42	WL852	F55137
Leiosphaeridia sp.	9A	175035	3	V44/2	WL872	F55138
Spongocystia eraduica	9B/C	175035	3	S34	WL747/48	F55139
Maculatasporites cf. *indicus*	9D	175035	2	R10/2	WL210	F55140
Cymatiosph. cf. *gondwanensis*	9E/F	175035	2	C25/3	WL393/94	F55141
Maculatasporites sp. 1	9G	175035	3	N28/4	WL724	F55142
Maculatasporites sp. 2	9H	175035	1	J29/4	WL54	F55143
Quadrisporites horridus	9I	175029	8	K36/1	WL153	F55144
microforaminiferal test lining	9L	175029	4	O32	WL1019	F55145
microforaminiferal test lining	9M	175035	10	N17/1	WL1046	F55146
scolecodont	9J	175029	9	E39	WL205	F55147
scolecodont	9K	175035	3	T37/3	WL774	F55165

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The impact of Pleistocene glaciations on population structure and systematics in five snake species in the Banda Arc islands of southern Wallacea: the views from genes, morphology and species assemblages

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Abstract

Wallacea is a region of geographic overlap in biotas derived from both Asian and Australasian continental plates. Species have also evolved rapidly over the last few (ca. 5) million years, aided by isolation and dynamic changes in island extents during the Pleistocene, to produce high levels of endemism. Vertebrate surveys on 26 islands some 30 years ago confirmed the high diversity of reptiles in the Inner and Outer Banda Arcs of Wallacea and numerous species endemic to the region. Here we assess the genetic relationships of island populations of five snake taxa (*Dendrelaphis inornatus, Coelognathus subradiatus, Lycodon capucinus, Psammodynastes pulverulentus, Trimeresurus insularis*) that we had previously examined using only morphological variables. Island heterozygosity is within the range generally reported for reptiles, although on the low side, consistent with their island location. One of the five species we examined, *Trimeresurus insularis*, shows a statistically significant decline in island mean heterozygosity from west to east, a phenomenon we have observed in some mammalian species in the Banda Arcs. Genetic data confirm speciation and endemism in the Banda Arcs within the genus *Dendrelaphis*. Populations on Kai and Yamdena islands on the Outer Banda Arc are genetically distinct from those on the islands to their west and are closely allied to the recently described *D. grismeri* from the Maluku islands. *Dendrelaphis pictus* occurs on Lombok and Nusa Penida, whereas *D. inornatus* spans the intervening islands of the Lesser Sunda Islands. Within all taxa, aggregations of island populations that are genetically alike are almost always geographically separated from genetically different groups by straits that persisted through the last Pleistocene glaciation. However, genetic differentiation is not invariably associated with these Pleistocene-persistent straits. Several snake species on Alor, on the Inner Banda Arc, are more closely allied to those on Timor and other Outer Banda Arc islands, and some on Sumba, within the Outer Banda Arc, are genetically closest to populations on the nearby Inner Banda Arc islands. The major separation of snake assemblages across Lesser Sunda Islands coincides with a Pleistocene-persistent sea barrier.

Keywords: biogeography, genetic diversity, islands, morphology, population structure, snakes, species assemblages, systematics, Wallacea

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INTRODUCTION

The loss of biodiversity, particularly among endemic species, is focal to international conservation efforts as we enter the sixth major global biodiversity extinction pulse in the world's evolutionary history (Ceballos *et al.* 2020). Conversely, understanding the mechanisms that foster the development of biodiversity and endemism, particularly among islands, is imperative to maintaining diversity and is essential to enhancing conservation efforts and management. Indonesia is amongst the most biodiverse countries in the world having the greatest number of mammal species, fourth highest number of bird species and third highest reptile diversity (McNeely *et al.* 1990). This enhanced diversity results from the country spanning two of the world's major biogeographic regions, the Australasian and the Asian, as well as covering two major tropical rainforest blocks, Borneo-Sumatra on the Asian tectonic plate and New Guinea on the Australian tectonic plate. Lying between these major blocks is Wallacea, a complex mosaic of islands that form a 'stepping-stone' corridor for species colonisation from the two main biogeographic regions and provides important opportunities for speciation amongst colonising taxa.

Wallacea, first proposed as a dynamic region in its own right by George Gaylord Simpson over 40 years ago (Simpson 1977; Ali & Heaney 2021), is now acknowledged for its high levels of vertebrate biodiversity and endemism as well as being one of the world's 35 major biodiversity hotspots (Myers *et al.* 2000). The southern islands of Wallacea (Fig. 1) are arranged in two adjacent arcs, the Inner and Outer Banda Arcs (IBA and OBA, respectively), arising from the collision of the Asian, Australian and Pacific continental plates (Veevers 1991). The western islands in the Banda Arcs comprise the Lesser Sunda Islands, so named for their close proximity to the major Sunda Islands of Sumatra, Borneo and Java on the Sunda Shelf. The high biodiversity and endemism across the islands of the Banda Arcs is a consequence of its tropical location, pronounced environmental gradients and the fragmentation of species populations on the myriad of islands in the region. The arrangement of islands in the Banda Arcs has also undergone change during the last Pleistocene glaciation as a consequence of fluctuating sea levels. These environmental circumstances, coupled with Wallacea's position between two of the major global biogeographic realms, highlights the potential for speciation, evolution, and adaptation within species populations. However, despite Wallacea having been a focus of zoogeographic research for over 160 years, Kitchener and colleagues described 28 new taxa across the Banda Arcs during 1987–1994 (Kitchener & Suyanto 1996).

The fauna of the Banda Arc islands has strong morphological and genetic patterning (Schmitt *et al.* 1995; Schmitt *et al.* 2009) and high endemism (Vane-Wright 1991; Kitchener & Suyanto 1996; How & Kitchener 1997; Zug 2010) with most island populations exhibiting strong links to those on adjacent islands. Nonetheless, speciation has occurred between populations that occupy adjacent islands in both Banda Arcs, especially those that remained permanently separated throughout the Pleistocene when sea levels fluctuated between glacial and interglacial periods. This differentiation between species populations is particularly pronounced in the molecular patterning amongst populations of both the fruit and insectivorous bat families. At the peak of the last Pleistocene glacial maxima around 18000 years bp, sea levels were up to 120 m below present levels (Lewis *et al.* 2013) and many of the Banda Arc islands, presently separated by shallow seas, were joined by land-bridges to form considerably larger composite islands (Heaney 1991).

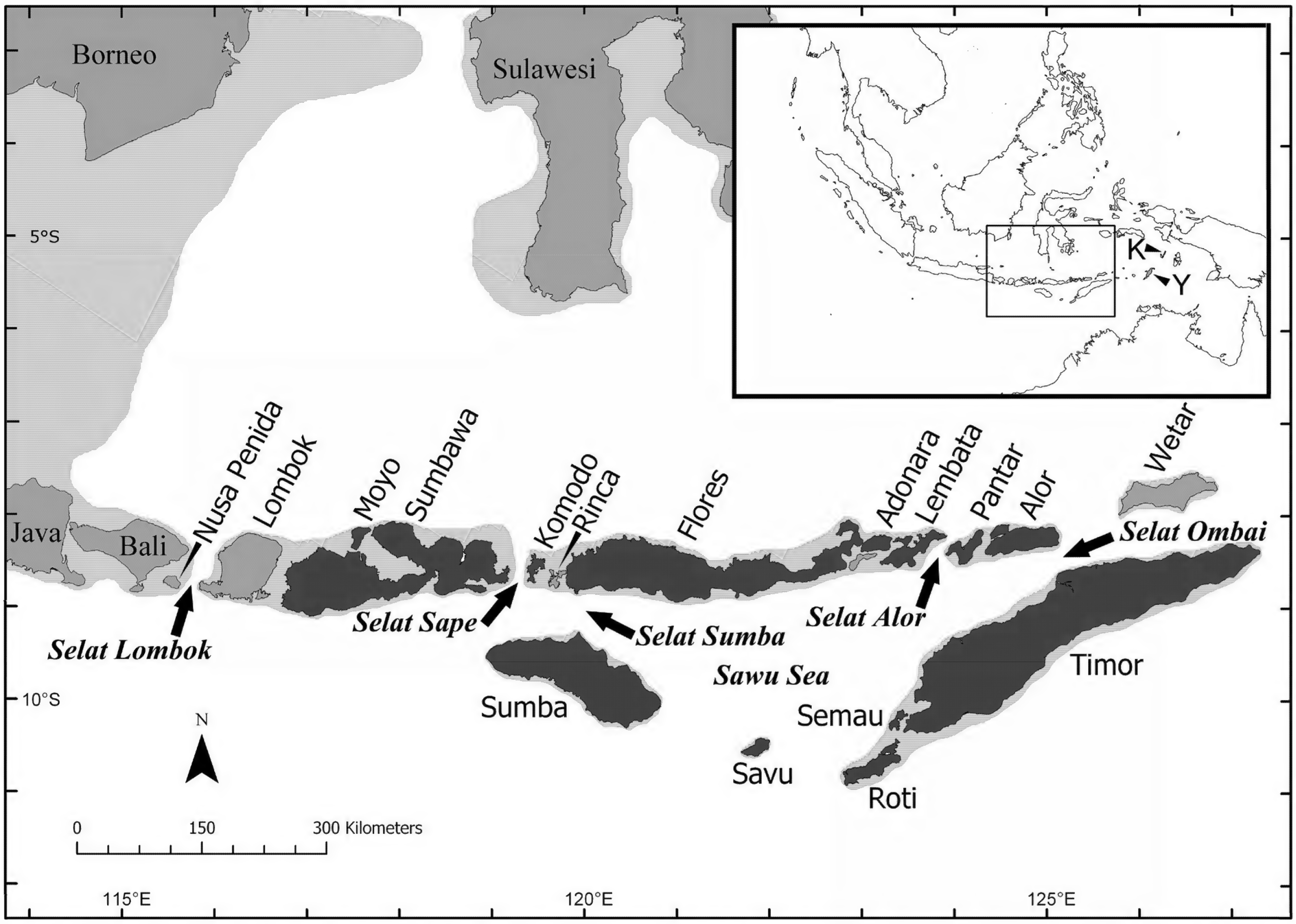


Figure 1. Regional island geography. Light shading indicates the maximum extent of islands and the Asian continent at the last Pleistocene glacial maximum. Arrows with italicized labels indicate the straits (selats) between sampled islands that persisted throughout the last Pleistocene glaciation. The 13 islands sampled for genetic analysis of the five taxa in this study have dark shading, with horizontal labels for Outer Banda Arc islands and angled labels for Inner Banda Arc islands. *Dendrelaphis* spp. on Nusa Penida, Lombok, Yamdena (Y in inset map) and Kai Besar (K) also were genetically assessed, and specimens from Rinca and Wetar were included in the species assemblage analysis.

The biogeographic relationship of snake faunas through the Indonesian islands indicates two principal groupings at both the generic and species level (How & Kitchener 1997). Those on Greater Sunda Islands on the Sunda shelf, Sulawesi and the Lesser Sunda Islands all are derived from Asia, whereas genera and species on islands of the southern and northern Maluku, West Irian and adjacent islands are more closely related to those in the Australo-Papuan region. Our previous work on morphological differentiation in five snake species across the Inner and Outer Banda Arcs (How *et al.* 1996a; How *et al.* 1996b) showed that populations on islands that remained separated throughout the Pleistocene had the highest morphological differentiation. However, in these snake and some mammalian taxa, this morphological differentiation was absent, or much reduced, in species that had good dispersal capabilities or were commensal with humans and easily transported (Kitchener & Suyanto 1996).

Important systematic research on the snake fauna of the Indonesian region in the last 20 years has highlighted the diversity of cryptic species in many of the genera through the region. Of particular relevance to the Lesser Sunda Islands are the reviews of *Trimeresurus* (David *et al.* 2003) and *Dendrelaphis* (van Rooijen & Vogel 2008; Vogel & van Rooijen 2008). In Indonesia both genera contain several taxa that show major geographic patterning. The molecular study of *Trimeresurus* confirmed the earlier findings of Giannasi *et al.* (2001) that the Lesser Sunda island form, *T. albolabris insularis*, warranted distinct specific status. The above revisions of the *Dendrelaphis pictus* complex from southeast Asia described new taxa for the Mollucca region and evaluated the systematic status of many species and subspecies across the complex's range. Additionally, a more recent evaluation of snake biogeography across the Lesser Sunda Islands (de Lang 2011) highlighted the high endemism (28%) within snakes of those islands and endorsed the biogeographic relationships described by How & Kitchener (1997). De Lang (2011, p. 50) also stated for the Lesser Sunda Islands that 'The taxonomy of several genera is uncertain and needs to be reviewed'. This state of flux in the taxonomy of many snakes can be extended to other reptilian genera across the whole Wallacean region (Schmitt *et al.* 2000; Zug 2010).

This study emanates from an extensive geographic assessment of variation in the distribution, morphology and genetics of terrestrial vertebrates from across the southern Wallacean region (Kitchener & Suyanto 1996; How & Kitchener 1997; Schmitt *et al.* 2009). Here we assess genetic variation in five snake taxa (Fig. 2) on the islands of the Lesser Sundas, a viperid (*Trimeresurus insularis*) and four colubrid (*Coelognathus subradiatus, Dendrelaphis inornatus, Lycodon capucinus* and *Psammodynastes pulverulentus*); nomenclature follows the Reptile Database (Utez *et al.* 2021). The geographic patterns in variation are interpreted in the context of the biogeographic setting, and especially related to the longevity of sea barriers during the Pleistocene glacial fluctuations. They are also compared with morphometric assessments of the same taxa. We also assess the snake assemblages on the Lesser Sunda Islands in light of new distributional information and recent changes in systematic determinations and interpret these within the context of their relationship to those in the broader Wallacean region. For all analyses, we assume the taxonomic status of *Dendrelaphis inornatus* (Boulenger 1897) and provide genetic evidence in support of that assessment.

MATERIALS AND METHODS

As part of a large survey between 1987 and 1993 (Kitchener & Suyanto 1996; How & Kitchener 1997), we sampled reptiles on 26 Wallacean islands in the Banda Arcs and the Sunda and Sahul Shelves. All specimen material and tissue reside in the collections of the Museum Zoolgicum Bogoriense or the Western Australian Museum. Unless otherwise noted, GENSTAT (VSN International 2020) was used for all statistical analyses.

Genetics

Genetic variation for the five species compared here—*Trimeresurus insularis, Coelognathus subradiatus, Dendrelaphis inornatus, Lycodon capucinus* and *Psammodynastes pulverulentus*—was assessed by allozyme electrophoresis on a cellulose acetate support medium according to Richardson *et al.* (1986) using liver tissue from 13 islands (Table 1; Appendix 1). Initially, we also assessed genetic variation in two geographically-adjacent cognates of *D. inornatus*; i.e. *D. pictus* from Nusa Penida (N = 2) and Lombok (N = 4), and *D. calligaster* from Yamdena (N = 2) and Kai Besar (N = 2). All four populations were excluded from further analysis because of their genetic differentiation from *D. inornatus* (see **Results**).

The extent of genetic variation within islands was assessed using mean unbiased expected heterozygosity (Nei 1978). Longitudinal trends in mean island heterozygosity were investigated using regression. Hierarchical *F*-statistics (Weir & Cockerham 1984) were used to estimate genetic variation between islands (F_{ST}), between localities within islands (F_{DS}), and within localities (F_{ID}) and tested for statistical significance using permutation (Excoffier 2003). To ascertain the interrelationships between populations as indicated by genetic data, genetic distances between island populations were estimated by the arc measure of Cavalli-Sforza & Edwards (1967) and subjected to principal coordinates analysis (PCO; Gower 1966).

Morphology

We undertook stepwise discriminant function analyses of our previously published morphological data (Appendix 2; How *et al*. 1996a; How *et al*. 1996b), limiting each taxon to those islands where genetic data were available. First, forward selection was used to obtain the four 'best' discriminating variables (based on minimizing Wilks' lambda) and then repeated using backward selection. From all variables selected by these two methods we used backward selection to obtain the best four variables to compute the final discriminant functions. The plots of island centroids on the first two discriminant functions were then examined and compared with their relative positions on the first two PCO coordinates. We also computed the correlations between the Mahalanobis

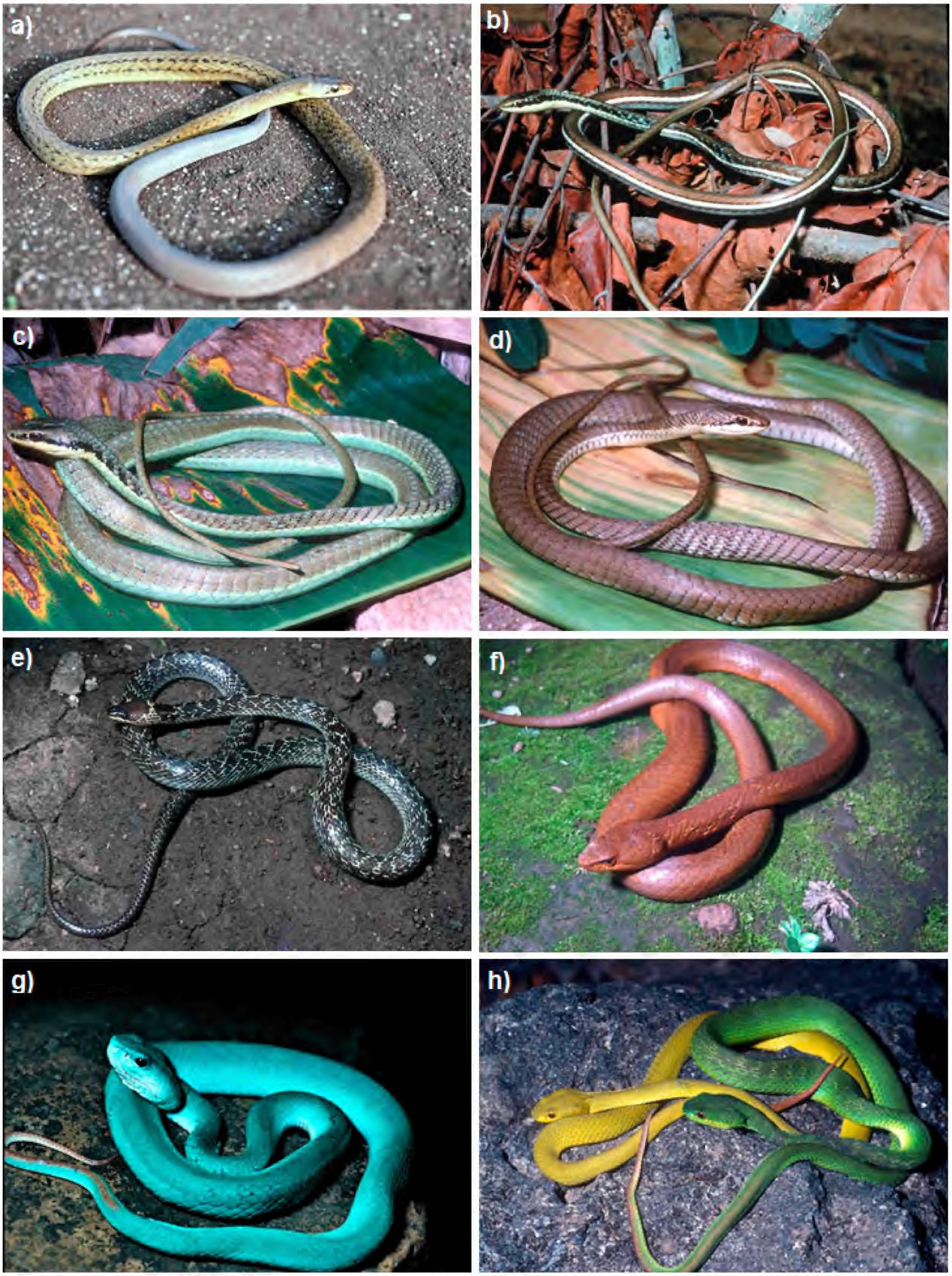


Figure 2. Images of the snake species evaluated with their location, island, and month and year of capture: **a)** *Coelognathus subradiata*, Waelonda Sumba, June 1989, [N Cooper]; **b)** *Dendrelaphis pictus*, Kuta Lombok, June 1988 [R Johnstone]; **c)** *Dendrelaphis inornatus*, Batu Tering Sumbawa, May 1988, [R Johnstone];. **d)** *Dendrelaphis inornatus*, Camplong Timor, October 1990 [R Johnstone]; **e)** *Lycodon capucinus*, Meraran Sumbawa, May 1988, [R Johnstone]; **f)** *Psammodynastes pulverulentus*, Robo Flores, May 1990, [R Johnstone]; **g)** *Trimeresurus insularis* (blue morph), Gn. Api Komodo, May 1990, [R Johnstone]; and **h)** *Trimeresurus insularis* (yellow and green morphs), Ilpokil Wetar, September 1993 [R How]. Square brackets indicate photographic credits.

and genetic distance matrices, and tested statistical significance using a modification of Mantel's test (Manly 2005).

Snake Assemblages

We assessed the biogeographic relationships of snake assemblages on 13 islands within southern Wallacea that had more than five snake taxa. This included 11 of the islands in the genetic study described above, and the nearby islands of Rinca and Wetar. We first constructed a species-by-island matrix of presence/absence of species and then used PRIMER E (Clarke & Gorley 2006) to cluster the matrix of Sorensen's similarity index using the unweighted pair group method with arithmetic mean (UPGMA) algorithm. The similarity profiling routine SIMPROF (Clarke *et al.* 2008) was used to determine statistically significant clusters and these relationships, along with relative similarity between islands—these are illustrated using non-metric multidimensional scaling (NMDS).

RESULTS

Dendrelaphis Systematics

Our initial analysis of the genetic relationship between island populations of *D. inornatus*, *D. pictus* and *D. calligaster*, confirmed that the latter was distinct on the first principal coordinate (Fig. 3a). After excluding *D. calligaster* and repeating the PCO analysis, *D. pictus* also appeared distinct from *D. inornatus* (Fig. 3b). Consequently, we only considered samples from the latter taxon in all further genetic and morphological analyses.

Genetic Diversity

Across all species, within-island mean heterozygosity was 3.4%, and 76% of islands had a mean less than 5% (Table 1). One species, *T. insularis*, showed a statistically significant relationship between mean heterozygosity and longitude (Fig. 4).

There were strong genetic differences between islands for three species, with F_{ST} much greater than zero (Table 2). This statistic was not significant in *L. capucinus* or *P. pulverulentus*, but the latter show statistically significant genetic differentiation between localities within islands (F_{DS}) and evidence of heterogeneity within localities (F_{ID}).

Principal coordinates analyses revealed the nature of the genetic relationships between island populations (Fig. 5, left frames). For all five species, the first two axes combined account for the majority of the variation, ranging from 59% to 93%, and generally provide a good reflection of the information in the genetic distance matrices.

Of the three species where there is statistically significant inter-island variation, *T. insularis* populations aggregate into three regional groups along the Banda Arcs (west, central and east; Fig. 5a). There are also three groups in *C. subradiatus*, one being the OBA islands, another of three IBA islands then Alor, which is distinct

Table 1. Island tissue sample size (N) and mean unbiased percent heterozygosity ($\overline{H}$). Islands are ordered from west to east within the Inner Banda Arc above the internal horizontal line, and the Outer Banda Arc below.

		Trimeresurus insularis		*Coelognathus subradiatus*		*Dendrelaphis inornatus*		*Lycodon capucinus*		*Psammodynastes pulverulentus*	
Island	**Code**	**N**	$\overline{H}$	**N**	$\overline{H}$	**N**	$\overline{H}$	**N**	$\overline{H}$	**N**	$\overline{H}$
Sumbawa	SW	13	7.0			10	7.7	1	0		
Moyo	MO					1	3.7	1	0		
Komodo	KO	1	8.0	1	0					1	3.4
Flores	FL	4	1.7	4	3.9	2	3.7	1	0	13	6.3
Adonara	AD							1	0		
Lembata	LE	9	2.1	3	2.9	7	5.3	1	3.8	4	5.9
Pantar	PA	2	0			2	3.7	3	4.4		
Alor	AL	12	0	3	2.9	14	2.6	11	3.9	6	4.6
Sumba	SB	6	1.2	4	1.7	3	3.2	6	3.6	2	7.5
Savu	SV					1	3.7				
Roti	RO					1	3.7	3	5.9		
Semau	SE	1	0	2	2.2			1	7.7		
Timor	TI	12	0.3	5	1.1	7	8.7				
Mean			2.3		2.1		4.6		2.9		5.5

Table 2. *F*-statistics for five snake species of the Lesser Sunda islands.

Species	F_{ST}	F_{DS}	F_{ID}
Trimeresurus insularis	0.59 ($p < 0.001$)	0.24 ($p = 0.052$)	0.15 ($p = 0.047$)
Coelognathus subradiatus	0.69 ($p = 0.003$)	0.11 ($p = 0.49$)	-0.22 ($p = 1$)
Dendrelaphis inornatus	0.62 ($p < 0.001$)	0.04 ($p = 0.67$)	-0.01 ($p = 0.58$)
Lycodon capucinus	0.10 ($p = 0.35$)	0.13 ($p = 0.30$)	-0.16 ($p = 0.96$)
Psammodynastes pulverulentus	0.26 ($p = 0.10$)	0.33 ($p = 0.002$)	0.27 ($p = 0.006$)

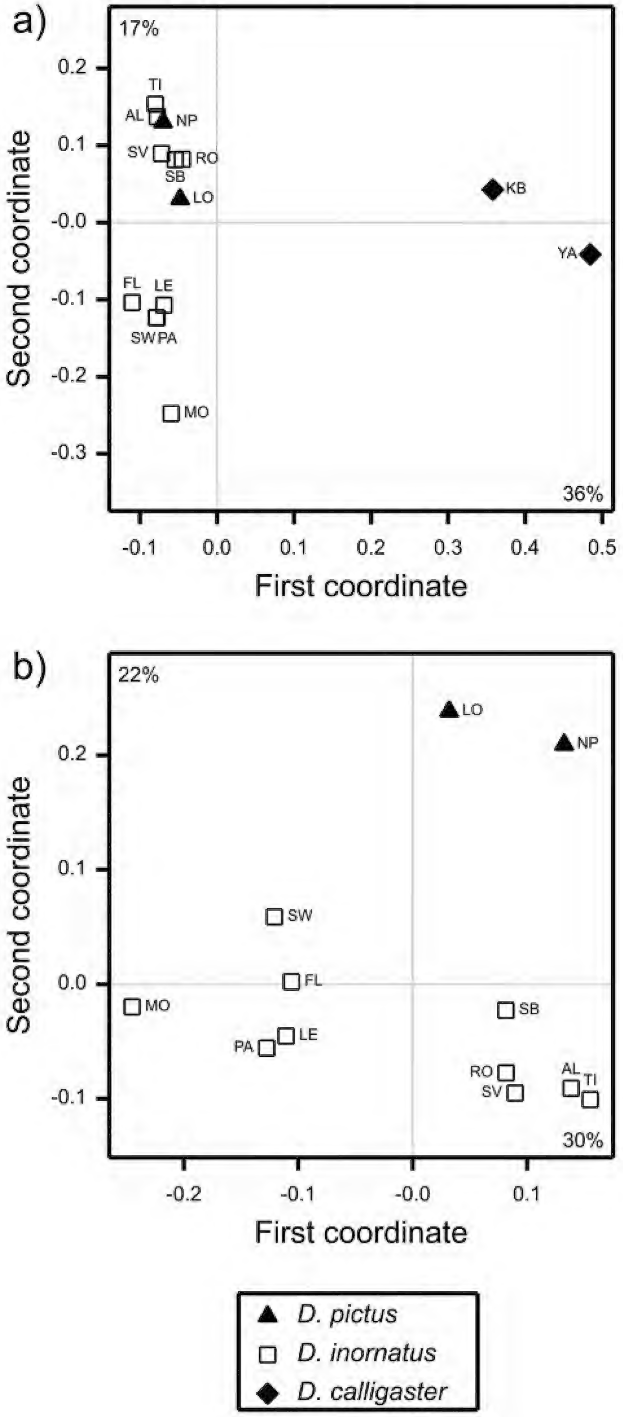


Figure 3. Plots of the first two axes from principal coordinates analysis of genetic distance between Wallacean island populations of *Dendrelaphis* spp.: **a)** island populations ascribed to *D. pictus*, *D. inornatus* and *D. calligaster*; and **b)** island populations ascribed to *D. pictus* and *D. inornatus*. Island codes in Table 1; KB = Kai Besar, YA = Yamdena.

from the other two (Fig. 5b). There is a marked separation into east and west groups of *D. inornatus* islands on the first axis. The eastern group, comprising all the OBA islands and Alor, show marked diversity on the second axis whereas the western group of IBA islands remains tightly aggregated on that axis (Fig. 5c). It is notable that the Alor population of these three species shows a greater affinity to the adjacent OBA islands than to those on the IBA. Considering these three species as a whole, the groupings that they exhibit, with one exception—the Roti population of *D. inornatus*—are separated by perennial sea barriers.

For the two species that do not have statistically significant F_{ST} values, *L. capucinus* and *P. pulverulentus*, the estimate is relatively large (especially so for the latter) and both hint at some genetic structure. The OBA islands of *L. capucinus* aggregate in one corner of the plot, with Alor and Pantar adjacent to that group and Sumbawa, the most western island, is marginal on the second axis (Fig. 5d). In *P. pulverulentus*, the one OBA island sampled, Sumba, is associated with its nearest IBA neighbour (Flores) whereas Alor is distinct from the other four islands sampled (Fig. 5e).

Genetics vs Morphology

The first two discriminant functions derived from morphological variables accounted for at least 80% of the inter-island variation in each species (Table 3). No species shows a significant correlation between genetic distance and morphological distance, although the estimates are higher and approach statistical significance for *Coelognathus* and *Dendrelaphis* compared to the other three species. A visual comparison of the morphology and genetic plots of the first two axes for *Coelognathus* (Fig. 5b) indicates a separation of the IBA and OBA islands in both. There are less obvious similarities in island relationships for genetic and morphological variation in *Dendrelaphis*, although Timor, Roti and Alor are marginal on the first axis for both plots (Fig. 5c). In general the two biological measures do not show many similarities in their geographic patterning.

Snake Assemblage Relationships

Two significantly distinct island groupings are currently identified in southern Wallacea on the basis of their snake assemblages (Fig. 6). A significantly divergent group is present on the islands of the western Inner Banda Arc (excluding Alor and Pantar, but including Sumba), while the other is on the islands on the Outer Banda Arc (excluding Sumba, but including Alor and Pantar).

DISCUSSION

Systematics

Bronzeback colubrid tree snakes (*Dendrelaphis* spp. complex) represent the only genera of the five examined that has a distribution extending from the Asian Sunda shelf to the Australasian Sahul shelf (Mertens 1934; How *et al.* 1996a; Vogel & van Rooijen 2008). *Dendrelaphis* populations on the Maluku islands of Yamdena, Kai and Ambon contain morphologically distinct taxa (How *et al.* 1996a) and could be assigned to the *D. calligaster* complex,

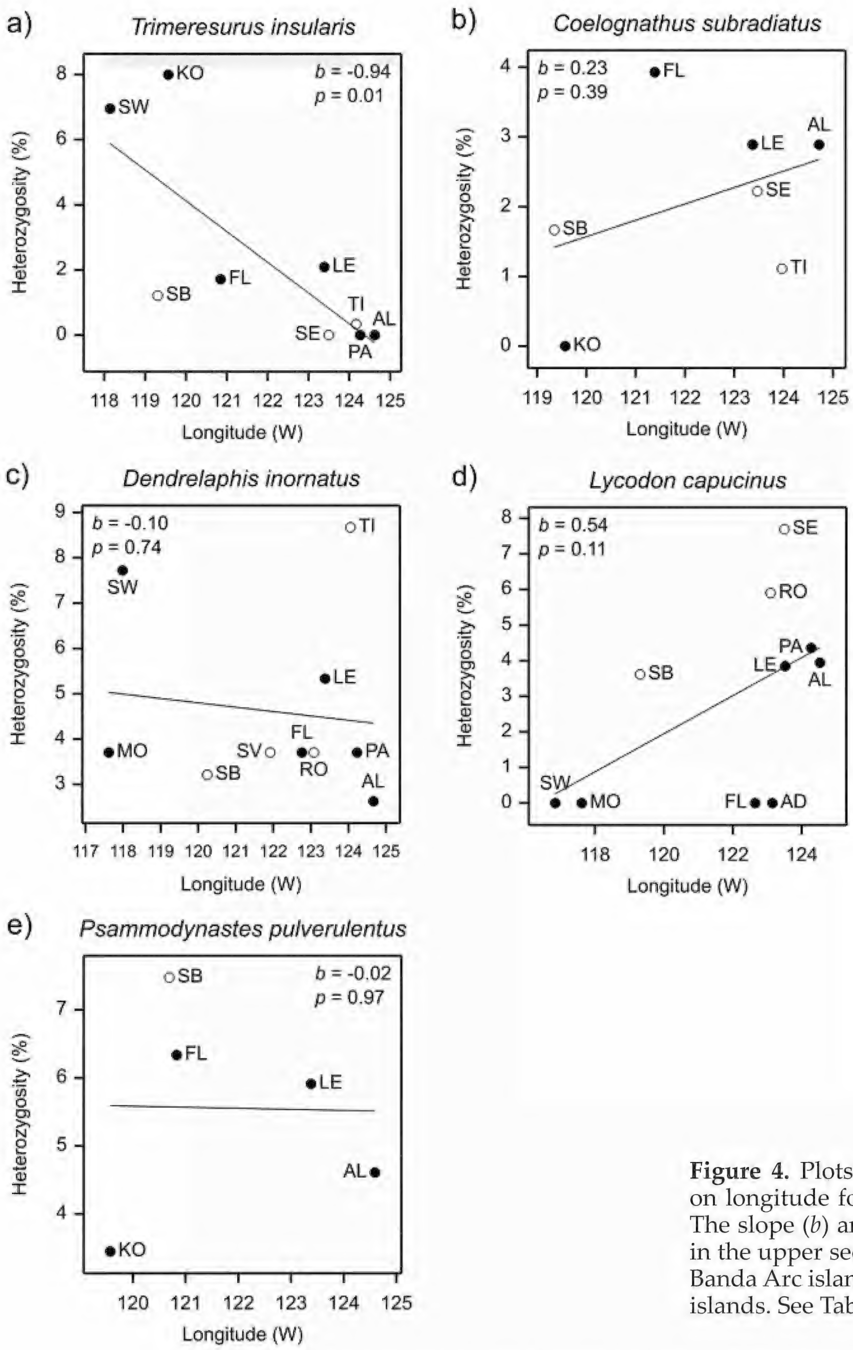
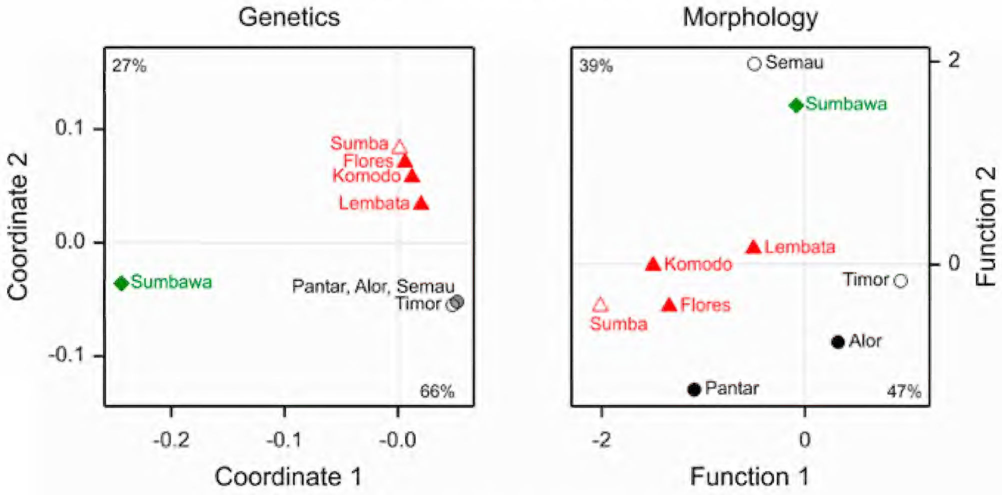


Figure 4. Plots of unbiased mean island heterozygosity on longitude for five taxa with the fitted regression line. The slope (*b*) and its statistical significance (*p*) are shown in the upper section of each plot. Filled symbols for Inner Banda Arc islands and open symbols for Outer Banda Arc islands. See Table 1 for the island codes.

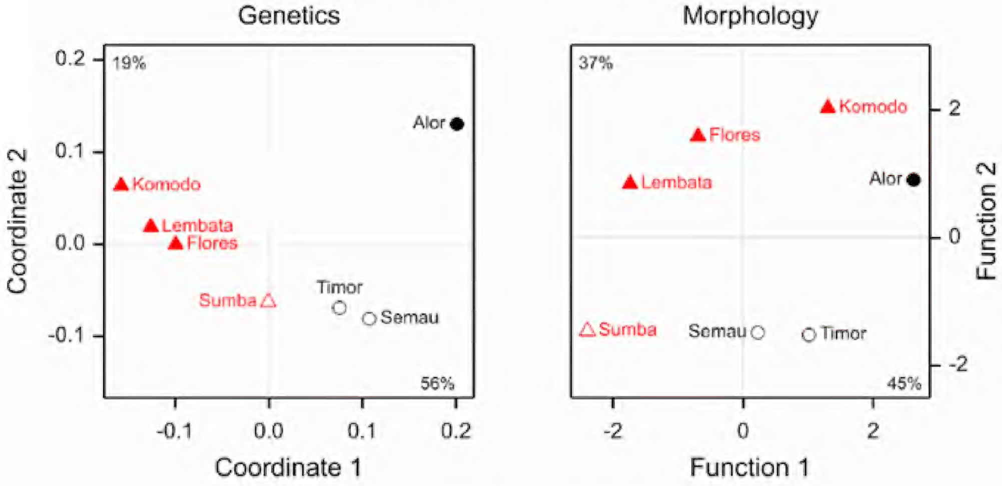
Table 3. The four morphological variables selected by stepwise discriminant function analyses, the variance accounted for (%) by the first two latent roots, and the correlation between the Mahalanobis distance matrix and the genetic distance matrix (*r*), with its statistical significance (*p*) for five snake species. See Appendix 2 for variable codes.

Species	**Selected variables**	**Function 1**	**Function 2**	***r***
Trimeresurus insularis	EYNAL, INNAW, NASL, PREOLO	47%	39%	0.06 ($p = 0.41$)
Coelognathus subradiatus	FROW, INNAL, LORV, PARL	45%	37%	0.39 ($p = 0.056$)
Dendrelaphis inornatus	INNAL, PARL, PREFW, ROSW	74%	15%	0.29 ($p = 0.069$)
Lycodon capucinus	EYED, FROL, PREFW, SUOCL	46%	34%	0.03 ($p = 0.42$)
Psammodynastes pulverulentus	FROW, INNAW, LORV, ROSW	60%	36%	-0.03 ($p = 0.29$)

a) *Trimeresurus insularis*



b) *Coelognathus subradiatus*



c) *Dendrelaphis inornatus*

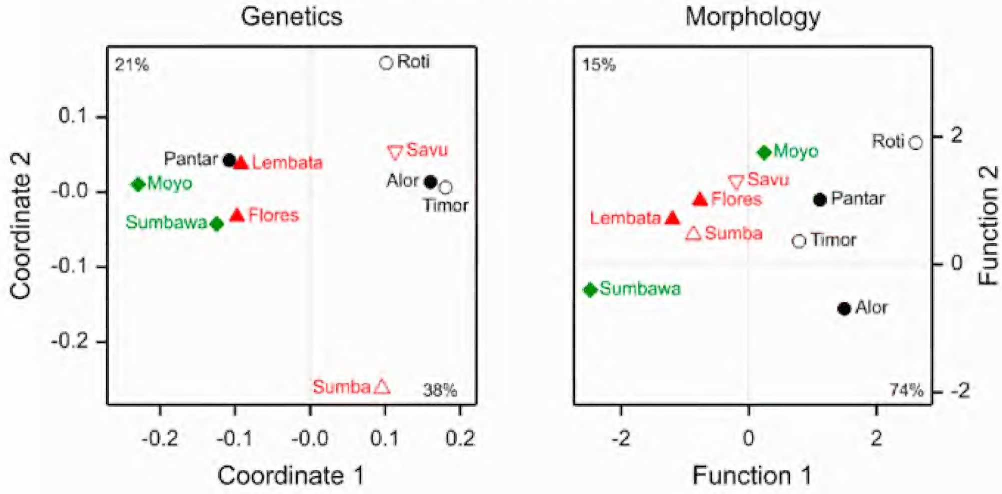
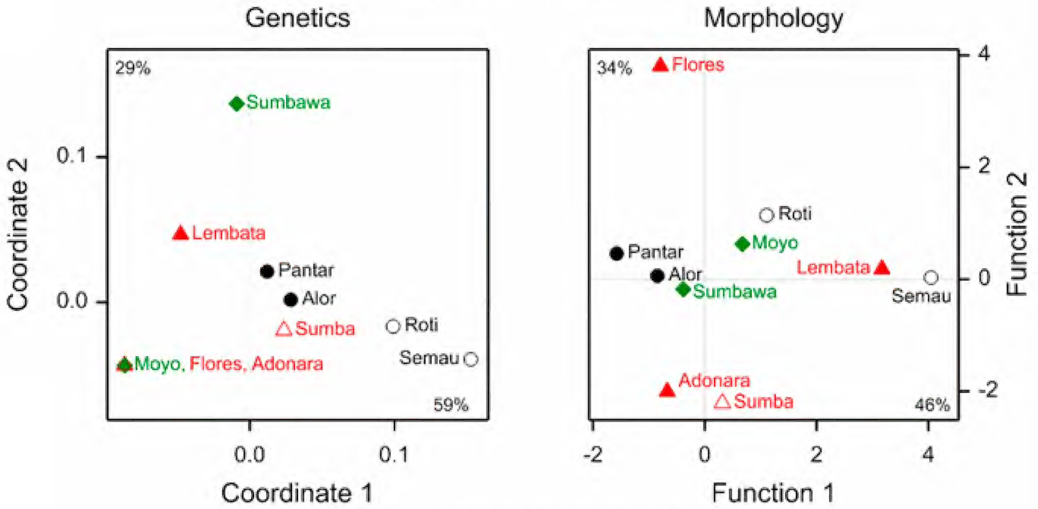


Figure 5. Plots of the genetic (left) and morphological (right) relationship of islands for five species. The genetic relationships represented are the first two coordinates from a principal coordinate analysis, and the morphological relationships are represented by the first two discriminant functions. The contribution to the total variation of each coordinate or function is shown at the upper end of each axis. Filled symbols for Inner Banda Arc islands and open symbols for Outer Banda Arc islands. Islands that were part of the same meta-island during the last Pleistocene glacial maximum share the same symbol and colour. Islands in the Outer Banda Arc have the same symbol and colour as the nearest Inner Banda Arc island (with the exception of ▽ for Savu).

d) *Lycodon capucinus*



e) *Psammodynastes pulverulentus*

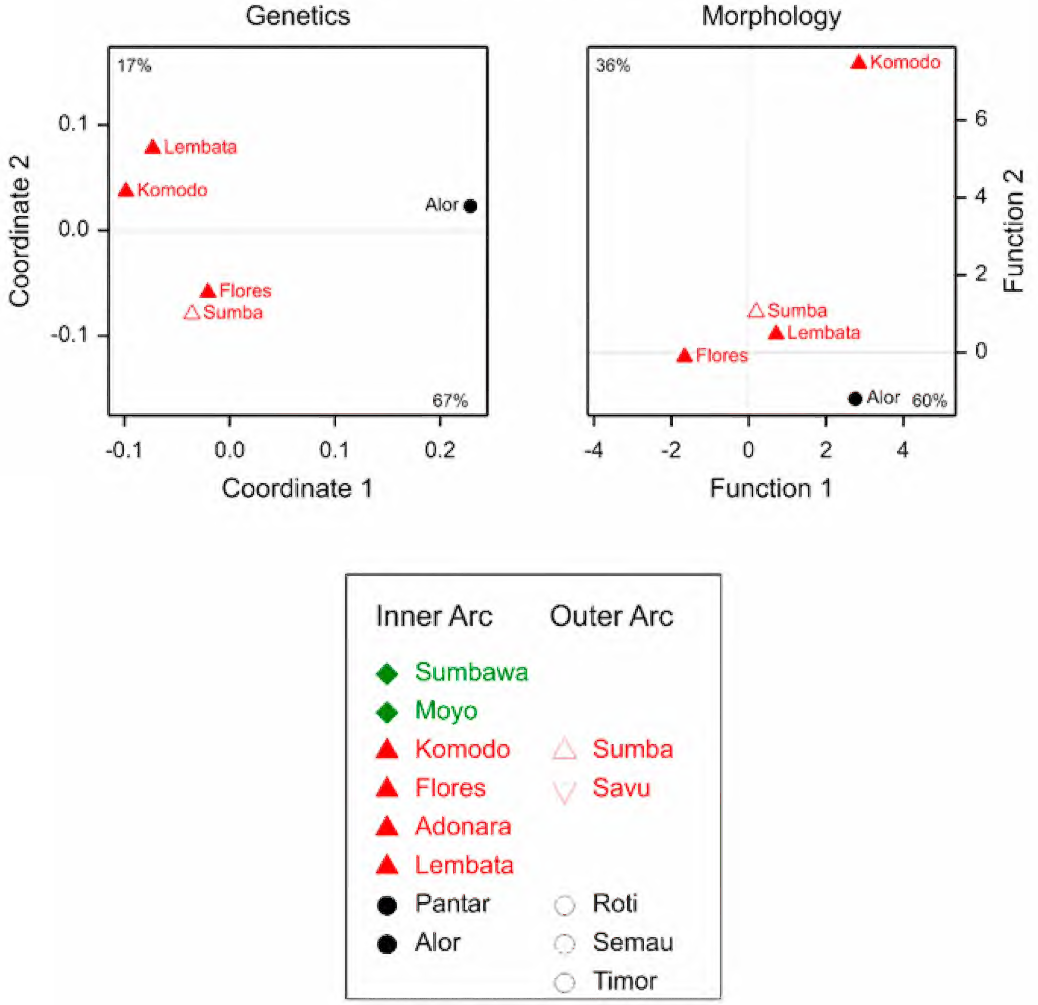


Figure 5. (Cont.)

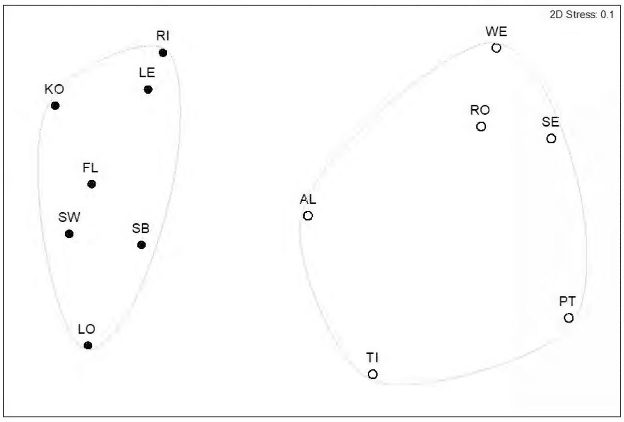


Figure 6. Non-metric multidimensional scale plot (NMDS) of snake assemblages from southern Wallacea, specifically islands across the Lesser Sundas that contain five or more snake taxa. The different symbols indicate significantly different groups of islands and the ellipses mark the 50% similarity groups. Island codes in Table 1; RI = Rinca, WE = Wetar. The two island groups are separated by the Sawu Sea on the Outer Banda Arc, and Selat Alor on the Inner Banda Arc; both straits persisted throughout the Pleistocence sea-level fluctuations.

later described as *D. grismeri* (Vogel & van Rooijen 2008), as all have 13 mid-body scale rows whereas all *Dendrelaphis* individuals on the Lesser Sunda Islands have 15 mid-body scale rows. How *et al.* (1996a) also indicated that the population on Kai Besar should be assigned to the described taxon *D. kaiensis,* but the population on Yamdena, in the Tanimbar Archipelago, differed significantly and probably represents a new taxon.

Our genetic study confirms that the *Dendrelaphis* spp. populations on the eastern OBA islands of Yamdena and Kai Besar are discrete taxa, probably with close affinities to *D. grismeri,* the taxon described from other Maluku islands (Vogel & van Rooijen 2008). Genetics also confirms two species of *Dendrelaphis* spp. (sensu *pictus*) are present along the Lesser Sunda Islands of southern Indonesia. The populations on Nusa Penida and Lombok islands represent the more widespread taxon of *D. pictus* (Fig. 4b) but are discrete from populations of *D. inornatus* along the remaining Lesser Sunda Islands.

Dendrelaphis pictus (sensu stricto) from the islands of south-eastern Indonesia was examined in morphological detail by Mertens (1934): he recognised *Dendrelaphis pictus pictus* on Bali and Lombok, but also extending onto Java and Sumatra; *D. p. inornatus* on Sumba, Timor and Alor; *D. p. intermedius* on Sumbawa and Flores; and considered *D. p. timorensis* on Timor was synonymous with *D. p. inornatus*. Our reappraisal of the morphology of *Dendrelaphis* populations from Bali and the Lesser Sunda Islands (How *et al.* 1996a) determined those on Bali, Nusa Penida and Lombok should be assigned to the widely distributed taxon, *D. pictus*, whereas those on the remaining islands of the Lesser Sundas should be referred to *D. inornatus*. This genetic study confirmed the specific status of *D. pictus* and *D. inornatus*, but also added molecular support for the morphological subspecies defined by Mertens (1934), with his *D. p. inornatus* on Sumba Timor and Alor, and *D. p. intermedius* on Sumbawa, Moyo, Flores, Lembata and Pantar.

The Rat Snakes, *Coelognathus* spp, are a wide-ranging and variable genus having the highest species richness for any colubrid genus and an extensive distribution (Schulz & Entzeroth 1996). Morphological differences in *Coelognathus* are such that the population on the Lesser Sunda Islands (*C. subradiatus*) warranted full specific status (in den Bosch 1985). Thus the Lesser Sunda Rat Snake, *C. subradiatus,* is endemic to the islands of the Lesser Sundas and consists of three discrete groups. The population on Alor is genetically distinct from those on other IBA islands of Komodo, Flores and Lembata, as well as from those on the OBA islands of Timor, Semau and Sumba, which are discrete from the IBA on the second axis of Figure 4b. This pattern of genetic separation resembles earlier morphology evidence (How *et al.* 1996b) that showed populations on Alor and Wetar were morphologically distinct from those on Timor+Semau+Sumba and are, in turn, distinct from those on Komodo+Flores+Lembata. However, these genetic data do not support the differentiation of the Sumba population, as implied by morphology (How *et al.* 1996b), but do show major genetic differentiation across several of the Pleistocene-persistent sea barriers. Recent genetic examination of *C. subradiatus* populations from the Lesser Sunda Islands using the ND4 gene (Reilly *et al.* 2021) defined three distinct clades (Alor, Wetar+Timor, Sumbawa+Flores). They postulate that the clades represent a species complex, supporting our earlier morphological study, but suggest more extensive examination is needed to confirm this speciation across the Lesser Sunda Islands.

The Wolf Snake, *Lycodon capucinus,* is widely distributed throughout southeast Asia, south-eastern China, the Philippines and Indonesia (except Borneo), and in this study showed limited genetic variation between island populations across the Lesser Sunda Islands—a finding supported by the limited mtDNA structure in the species throughout its range (Reilly *et al.* 2019). This lack of genetic patterning is consistent with the morphology (How *et al.* 1996b), and its known distribution and ecological parameters. *Lycodon capucinus* is recognised as a rapid coloniser (Smith 1998) of new environments and easily transported from one island to another by human activity (Leviton 1965; Reilly *et al.* 2019). These ecological characteristics are reflected in its relatively undifferentiated island populations in both morphological and genetic space.

The Mock Viper, *Psammodynastes pulverulentus,* has the widest distribution of all species examined in this study, extending from north-eastern India, throughout southeast Asia, southern China, Taiwan, the Philippines and in Indonesia as far east on the IBA as Alor (de Lang 2011). However, on the OBA islands it only occurs on Sumba. Genetic data indicates a distinct separation of the population on Alor, in accordance with our earlier morphological study (How *et al.* 1996b).

The White-lipped Island Pit Viper, *Trimeresurus insularis*, extends from eastern Java onto the Lesser Sunda Islands, with its easternmost record from the island of Kisar (David *et al.* 2003) and it showed limited morphological variation along the island chains of eastern Indonesia (How *et al.* 1996b). Malhotra &Thorpe (1997) concluded that a complex phylogenetic pattern existed within *Trimeresurus* in Indonesia such that species and their relationships were difficult to determine using morphological and molecular techniques. Within *T. insularis*, the mtDNA patterns of island populations did not correspond with morphological patterns (Malhotra and Thorpe *op. cit.*), making the differentiation of taxa impossible using morphological techniques alone. The later study by David *et al.* (2003) indicated that there was limited mtDNA separation of populations between Java and Wetar despite reporting a Java clade, a Flores clade and a Komodo to Alor clade. Reilly *et al.* (2019) explored mtDNA sequences in the species across the Lesser Sundas and showed low genetic diversity with Lombok forming a monophyletic group, but supported by just one mutation. The present study indicates a genetic difference only in the Sumbawa population.

Important revisions of reptile taxa across the Lesser Sunda Islands, indicate that many have 'species' level differences based solely on morphological criteria. The widely distributed colubrid tree snake, *Boiga cynodon*, has been revised using both morphology and genetics (Ramadhan *et al.* 2010; Weinell *et al.* 2021), and determined to have a Lesser Sunda endemic species, *Boiga hoeseli*. Wüster &Thorpe (1989) revised the Asiatic Cobra, *Naja sputatrix,* a species that extends along much of the IBA (de Lang 2011), and detected three morphologically distinct groups: the populations on Komodo and Flores differ from those to the west on Sumbawa through to east and central Java, and in turn these differed from the western Java population. The morphological documentation of subspecific separation in the volant agamid, *Draco volans,* across the islands of Nusa Tenggara (Musters 1983) is remarkably similar to the morphologic differentiation of subspecies determined for *Dendrelaphis pictus* (Mertens 1934). Separation in *Draco* occurred somewhere between Adonara and Alor on the IBA, and Sumba and Roti on the OBA. Similarly, How *et al.* (1998) determined that the skink *Emoia* on Sumba was morphologically distinct from *Emoia similis* on Flores and Komodo and represented an endemic taxon.

Genetic diversity

At 3.4%, mean heterozygosity within the five taxa we examined is generally a little lower than the 5–7% typically reported in reviews of reptilian studies (Nei 1975). However, most studies are of continental populations and it is well known that island populations generally have lower levels of genetic diversity than their mainland counterparts, so these five taxa seem to have typical levels of genetic diversity given their insular locations.

We previously reported that some Lesser Sunda mammalian species of Asian origin show a decline in heterozygosity from west to east (Schmitt *et al.* 2009). In the present study we observed this in *Trimeresurus insularis* but not in the other four species. Determining the cause of such trends is problematic. An obvious explanation is that population sizes may decline from west to east but that leaves the question of what may cause this trend. There are known environmental gradients from west to east, such as decreasing rainfall and increasing woodland habitats, that may be driving heterozygosity directly or via population size, but we have virtually no information that could lead to a credible explanation.

Our observation of strong genetic differences between islands for three species is most likely, in our view, to be the consequence of restricted gene flow between islands and the consequent impact of random genetic drift. Nonetheless, we cannot exclude differential natural selection, although variation in the loci we have utilized is, typically, ascribed to a balance between gene flow and genetic drift.

A balance between gene flow and genetic drift as a major cause of genetic diversity among islands is supported by an association between the degree of inter-island genetic differentiation and the type of sea barrier between the islands—in general, genetically-determined island groups are separated by sea barriers that persisted throughout the Pleistocene. Genetic differentiation across Selat Alor seems to be particularly strong and suggests this strait has constrained gene flow in all five species with Alor populations being distinct from their IBA cognates. We have constructed a somewhat subjective summary of the impact of the Pleistocene-persistent straits on genetic differentiation for each species to illustrate the extent of this generality (Table 4).

Such barriers, however, do not inevitably lead to strong genetic differentiation. The Sumba populations of *Trimeresurus, Lycodon* and *Psammodynastes* all have strong affinity with Sumbawa, despite separation by the large Selat Sumba. The wide Selat Ombai also appears to be a relatively weak barrier to gene flow for *Dendrelaphis, Trimeresurus* and *Lycodon*, with their Alor populations showing close affinity with Timor and the other OBA islands.

Islands separated by ephemeral sea barriers—those that disappeared during Pleistocene glacial maxima—almost always contain genetically similar faunas. A notable exception is the Roti population of *Dendrelaphis*, which is distinct from Timor's (although the sample size of the former was only one) and these two populations occupy similar positions on the first PCO coordinate. Similar observations and conclusions can be made for the differentiation of the Flores population of *Psammodynastes* compared to that from Komodo and Lembata.

Morphological island relationships

This study provides modest evidence for a correlation between genetic and morphological pattern in *Dendrelaphis* and *Coelognathus* populations across the Lesser Sunda Islands. The lack of a significant correlation between the genetic and morphological patterns for the other three genera illustrates the importance of combining both measures of variation in order to be confident of population level differences that may translate to taxonomic separation.

The genetic and morphological appraisal of two skink species along the Banda Arcs of eastern Indonesia (Schmitt *et al.* 2000) showed that genetic variation was not matched by similar separation in morphological characters in either taxa. They suggested that sibling taxa may be evolving in the Lesser Sunda Islands, which were not detectable morphologically. The wide-ranging skink *Mabuya multifasciata*, showed little morphological or genetic variation along the Banda Arcs; however, a

Table 4. Summary of the effects of Pleistocene sea barriers on the population structure of five snake species.

Species	Selat Sape	Selat Alor	Selat Sumba	Sawu Sea	Selat Ombai
Trimeresurus insularis	++	++	0	++	0
Coelognathus subradiatus		++	+	+	++
Dendrelaphis inornatus	0	++	++	?	?
Lycodon capucinus	+	+	0	?	0
Psammodynastes pulverulentus		++	0		

Note: + and ++ indicate weak and strong differentiation across a barrier; 0 indicates no differentiation; ? indicates variable or uncertain differentiation. Empty cells indicate no assessment was possible.

similarly wide-ranging skink, *Lamprolepis elberti*, showed a genetic separation between populations on the Lesser Sunda Islands that was not matched by morphological characters such that cryptic species probably existed. Morphologically conservative but genetically distinct taxa have also been recorded in the skink genera *Emoia* (Bruna *et al*. 1996) and *Lipinia* (Austin 1995) on islands in the Pacific Ocean.

Biogeography of snake assemblages

Biogeographic relationships of 36 islands in the Indonesian archipelago, using land and freshwater snakes (How & Kitchener 1997), documented two main groups incorporating: (1) the Greater Sunda Islands, the Lesser Sunda Islands, Sulawesi and the Banggai and Sula archipelagos; and (2) the islands of northern and southern Maluku, New Guinea and adjacent islands and Australia. The former group contains principally Asian snake genera and species, whereas Australo-Papuan genera and species dominate in the latter. This major division in snake faunas is evident between the islands of Maluku in the east and Sulawesi and the Lesser Sunda Islands in the west, indicating the major boundary in the snake fauna of Indonesia is Weber's Line, rather than Wallace's Line. Holloway (2003) reanalysed How and Kitchener's data, and their results agreed, for the greater part, with those published earlier.

The present reappraisal of biogeographic relationships of islands of southern Wallacea is based on their snake assemblages using currently determined distributions of species and their taxonomy. Within the Lesser Sunda Islands, the IBA islands of Alor and Wetar have snake faunas more similar to Savu, Roti, Semau and Timor on the OBA, than to the more westerly Lesser Sunda Islands of Sumbawa, Moyo, Komodo, Flores, Lembata and Pantar that are also IBA islands. However, the Sumba fauna on the OBA is more closely allied to that on proximal IBA islands than to any other OBA island. This paper provides strong support to Alor linking with OBA islands, except Sumba, as described by How & Kitchener (1997), although it does not support their separation of Lembata, Flores and Komodo from either Pantar, Sumba or Sumbawa.

CONCLUSIONS

By the nature of its geographic location and extent, Wallacea's biota is subjected to an island environment and high insularity. The region is geologically young and has experienced variations in sea-level of up to 120 m associated with recent Pleistocene glaciations that influenced island size and connectivity. The glacial cycles led to the coalescence of some islands as sea-levels declined during cooler periods and, conversely, the fragmentation of larger composite islands during warmer periods. These fluctuations in island arrangements facilitated evolution of many endemic species throughout the region. Isolation by straits that persisted throughout the Pleistocene seems, at least for less mobile species, to be a primary cause of their population structure, whereas the genetic affinities of island populations separated by ephemeral straits is generally much greater. Consequently, significant differentiation occurs in most Wallacean vertebrates separated by persistent sea barriers over the last two million years, giving rise to populations with high local endemism that are important for active conservation management.

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Appendix 1. Allele frequencies in five snake species of southern Wallacea.

Trimeresurus insularis

		Sumbawa	Komodo	Flores	Lembata	Pantar	Alor	Sumba	Semau	Timor
ACYC	*a*	0.88	1	1	1	1	1	1	1	0.96
	b	0.12								0.04
ME2	*a*	0.17								
	b	0.29	0.50	0.25	0.56	1	1	0.17	1	1
	c	0.54	0.50	0.75	0.44			0.83		
ME3	*a*		1	1	1	1	1	1	1	1
	b	1								
PEP C	*a*	0.54								
	b	0.46	1	1	1	1	1	1	1	1
6PGD	*a*	0.77								
	b	0.23	0.50	1	1	1	1	1	1	1
	c		0.50							
	N	13	1	4	9	2	12	6	1	12

The following loci were invariant: *ACON1, ACON2, ACP1, ACP2, ADA, ENOL, FDP, GOT1, GOT2, aGPD, IDH1, IDH2, LDH1, LDH2, MDH1, MDH2, ME1, PEP A, PGM1, PGM2.*

Coelognathus subradiatus

		Komodo	Flores	Lembata	Alor	Sumba	Semau	Timor
GDA	*a*				0.33			
	b	1	1	1		1		0.17
	c				0.67		1	0.83
IDH2	*a*	1						
	b		1	1	1	1	0.50	1
	c						0.50	
ME1	*a*	1	0.88	1	1	1	1	1
	b		0.12					
ME2	*a*				0.83			
	b	1	1	1	0.17	1	1	1
PEP B	*a*					0.12		
	b	1	1	1		0.88	1	1
	c				1			
PEP C1	*a*	1	1	0.83	1	1	1	1
	b			0.17				
6PGD	*a*		0.12		1	1	1	1
	b	1	0.88	1				
PGM1	*a*					0.12		
	b		0.12					
	c	1	0.88	1	1	0.88	1	1
	N	1	4	3	3	4	2	5

The following loci are invariant: *ACON1, ACON2, ACP, ACYC, ADA, ENOL, GOT1, GOT2, aGPD1, aGPD2, IDH1, LDH1, LDH2, MDH1, MDH2, ME3, NP, PEP A, PEP C2, PEP C3, PEP D, PGM2.*

***Dendrelaphis* spp.**

		Nusa Penida	**Lombok**	**Sumbawa**	**Moyo**	**Flores**	**Lembata**	**Pantar**	**Alor**	**Sumba**	**Savu**	**Roti**	**Timor**	**Yamdena**	**Kai Besar**
ACON1	*a*	1	1	0.2											
	b			0.8	1	1	1	1	1	1	1	1	1	1	1
ACON2	*a*							0.25							
	b									0.33			0.07		
	c	0.25							1		1	1	0.93		
	d	0.75	1	1	1	1	1	0.75		0.67					
	e													1	
	f														1
ENOL	*a*													1	1
	b	1	1	1		1	1	1	0.96	1	1	1	0.93		
	c				1				0.04				0.07		
FDP	*a*	1	1	1	1	1	1	1	1	1	1	1	1		1
	b													1	
GDA	*a*													1	1
	b		0.125	0.1											
	c	0.5	0.875	0.8	1	1	1	1	1	1	1	1	1		
	d			0.1											
	e	0.5													
GOT2	*a*	1	1	1	1	1	1	1	1		1	1	1		
	b									1					
	c													1	
	d														1
GPI	*a*	1	1	1	1	1	1	1	1		1	1	1	1	1
	b									1					
GPT	*a*						0.57		0.04						
	b		0.25	0.95	1	1									
	c						0.36	1							
	d	0.75	0.75	0.05			0.07		0.96	1	1	1	1	1	1
	e	0.25													
IDH2	*a*													1	1
	b	1	1	1	1	1	1	1	1	1	1	1	1		
MDH1	*a*						0.36	0.25						1	1
	b	1	1	1	1	1	0.64	0.75	1	1	1	1	0.93		
	c												0.07		

***Dendrelaphis* spp. (Cont.)**

		Nusa Penida	Lombok	Sumbawa	Moyo	Flores	Lembata	Pantar	Alor	Sumba	Savu	Roti	Timor	Yamdena	Kai Besar
NP	*a*	1	1	1	1	1	1	1	1	1	1	1	0.86	1	1
	b												0.14		
PEP A	*a*													0.75	
	b		0.12												
	c			0.8	0.5									0.25	
	d	1	0.88	0.2		1	1	1	1	1	1	1	1		1
	e				0.5										
PEP B	*a*											1			
	b			0.9	1	1	1	1	1	1	1		1		
	c	1	0.38												
	d		0.62	0.1										1	1
PEP C	*a*												0.21		
	b	1	1	1	1	1	1	1	1	1	1	0.5	0.71	1	1
	c											0.5			
	d												0.07		
PEP D1	*a*			0.05											
	b		0.12	0.45	1	0.5	1	1			0.5	1		0.5	0.5
	c	1	0.38	0.5		0.5			1	1	0.5		0.93	0.5	0.5
	d		0.5										0.07		
PEP D2	*a*	1	1	1	1	1	1	1	0.61	0.83	1	1	0.36	1	1
	b								0.39				0.64		
	c									0.17					
6PGD	*a*			0.1											
	b														0.25
	c												0.29		
	d	1	1	0.9	1	1	1	1	0.96	1	1	1	0.64	1	0.75
	e								0.04						
	f												0.07		
SORDH	*a*		0.25				0.21								
	b	1	0.75	1	1	1	0.79	1	1	1	1	1	1		1
	c													1	
	N	2	4	10	1	2	7	2	14	3	1	1	7	2	2

The following loci were invariant: *ACP, GAPD, GOT1, LDH1, LDH2, MDH2, PGAM, PGM, SOD.*

Lycodon capucinus

		Sumbawa	Moyo	Flores	Adonara	Lembata	Pantar	Alor	Sumba	Roti	Semau
ADA	*a*	1	1	1	1	1	0.67	0.46	0.42	0.5	
	b						0.33	0.54	0.58	0.5	1
IDH1	*a*	1				0.5	0.5	0.41	0.25	0.5	0.5
	b		1	1	1	0.5	0.5	0.59	0.75	0.5	0.5
IDH2	*a*									0.83	0.5
	b	1	1	1	1	1	1	1	1	0.17	0.5
	N	1	1	1	1	1	3	11	6	3	1

The following loci were invariant: *ACON1, ACON2, ACP, ENOL, GDA, GOT, GPI, aGPD, LDH1, LDH2, MDH1, MDH2, ME, MPI, NP, PEP A, PEP B, PEP C, PEP D, 6PGD, PGM1, PGM2, SORDH.*

Psammodynastes pulverulentus

		Komodo	Flores	Lembata	Alor	Sumba
ACYC	*a*		0.04			
	b	1	0.96	1	1	1
GDA	*a*	1	1	0.88	1	1
	b			0.12		
GPT	*a*	1	0.73	0.62	0.17	0.5
	b		0.27	0.38	0.83	0.5
IDH2	*a*	1	0.96	0.88	0.83	1
	b		0.04	0.12	0.17	
LDH2	*a*	1	1	1		1
	b				1	
NP	*a*	1	0.81	1	0.9	1
	b		0.19		0.1	
PEP C2	*a*	1	0.96	1	1	1
	b		0.04			
PEP C3	*a*	1	0.81	0.75	0.42	0.75
	b		0.19	0.25	0.58	0.25
PEP D	*a*					0.25
	b	0.5	0.81	0.12	1	0.75
	c	0.5		0.88		
	d		0.19			
6PGD	*a*		0.04			
	b	1	0.92	1	1	1
	c		0.04			
PGM1	*a*		0.04		1	
	b	1	0.96	1		1
SORDH	*a*					0.25
	b	1	1	1	1	0.75
	N	1	13	4	6	2

The following loci were invariant: *ACON1, ACON2, ACP, ADA, ENOL, GLDH, GOT1, GOT2, aGPD, IDH1, LDH1, MDH1, MDH2, PEP A, PEP B, PEP C1, PGM2.*

Gene codes

Code	**Enzyme**
ACON	Aconitase
ACP	Acid phosphatase
ACYC	Acyclase
ADA	Adenosine deaminase
ENOL	Enolase
FDP	Fructose-1,6-diphosphatase
GAPD	Glyceraldehyde-3-phosphate dehydrogenase
GDA	Guanine deaminase
GLDH	Glutamate dehydrogenase
GOT	Aspartate aminotransferase
aGPD	Glycerol-3-phosphate dehydrogenase
GPI	Glucose-phosphate isomerase
GPT	Alanine aminotransferase
IDH	Isocitrate dehydrogenase
LDH	Lactate dehydrogenase
MDH	Malate dehydrogenase
ME	Malic enzyme
MPI	Mannose-phosphate isomerase
NP	Nucleoside phosphorylase
PEP A	Peptidase A
PEP B	Peptidase B
PEP C	Peptidase C
PEP C1	Peptidase C1
PEP C2	Peptidase C2
PEP C3	Peptidase C3
PEP D	Peptidase D
PEP D1	Peptidase D1
PEP D2	Peptidase D2
6PGD	6-phosphogluconate dehydrogenase
PGAM	Phosphoglycerate mutase
PGM	Phosphoglucomutase
SOD	Superoxide dismutase
SORDH	L-iditol dehydrogenase

Appendix 2. Morphometric features measured for five snake species (How *et al*. 1996a; How *et al*. 1996b).

Morphometric	**Code**	***Trimeresurus insularis***	***Coelognathus subradiatus***	***Dendrelaphis inornatus***	***Lycodon capucinus***	***Psammodynastes pulverulentus***
Snout to vent length	SVL	✓	✓	✓	✓	✓
Tail length	TAIL	✓	✓		✓	✓
Ventral scale count	VENT	✓	✓	✓	✓	✓
Sub-caudal scale count	CAUD	✓	✓		✓	✓
Eye diameter	EYED	✓	✓	✓	✓	✓
Eye-nostril length	EYEN		✓	✓	✓	✓
Eye-nasal scale length	EYNAL	✓				
Frontal medial suture length	FROL		✓	✓	✓	✓
Frontal width	FROW		✓	✓	✓	✓
Internasal medial suture length	INNAL	✓	✓	✓	✓	✓
Internasal width	INNAW	✓	✓	✓	✓	✓
Length of upper labial one	LAU1	✓				
Length of upper labial two	LAU2	✓				
Length of upper labial three	LAU3	✓				
Loreal dorsal margin length	LORD		✓	✓	✓	✓
Loreal ventral margin length	LORV		✓	✓	✓	✓
Loreal diagonal length	LORL				✓	
Nasal length	NASL	✓				
Parietal length	PARL		✓	✓	✓	✓
Prefrontal medial suture length	PREFL		✓	✓	✓	✓
Prefrontal width	PREFW		✓	✓	✓	✓
Lower preoculars length	PREOLO	✓				
Upper preoculars length	PREOUP	✓				
Dorsal rostral width	ROSD	✓				
Ventral rostral width	ROSV	✓				
Rostral height	ROSH	✓				
Rostral width	ROSW		✓	✓	✓	✓
Subocular length	SUBOL	✓				
Superocular length	SUOCL	✓	✓	✓	✓	
Maximum superocular width	SUOCW	✓	✓		✓	
Scale count between superoculars	SUPSUP	✓				
Width of the head between the superoculars	SUPSUPW	✓				
Supralabial six length at mid-height	UL6			✓		
Supralabial seven length at mid-height	UL7			✓		

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The distribution of the threatened Black-striped Burrowing Snake (*Neelaps calonotos*) in the Perth region, Western Australia

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The Black-striped Burrowing snake *Neelaps calonotos* is a small fossorial elapid restricted to the coastal habitats of the Swan Coastal Plain between Dawesville and Port Denison in southwestern Australia. A large portion of its range lies within the Perth region, where rapid urban development and associated habitat loss poses the greatest threat to the continued survival of remaining populations. Consequently, populations have been rendered sparse and uncommon, especially within the southernmost limits of its range. This short appraisal of the currently known distribution of *N. calonotos* within the Perth region indicates further surveys would be helpful to conserve the species and expand our understanding of the species' distribution within an increasingly urbanised environment.

Keywords: *Neelaps calonotos*, elapid snake, threatened fauna, urban development

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INTRODUCTION

The Black-striped Burrowing Snake, *Neelaps calonotos*, (Fig. 1) is one of five species of small burrowing elapids in the Perth region and is listed as 'Priority Three' under State legislation (Department of Parks and Wildlife 2015), whereas the International Union for Conservation of Nature (IUCN) lists it as Near Threatened (Gaikhorst *et* al. 2018). The Priority Three listing according to the Department of Biodiversity, Conservation and Attractions (2019, p. 3) is granted for 'species that are known from several locations', where there exists 'significant remaining areas of apparently suitable habitat, much of it not under imminent threat'.

The biology of *N. calonotos* is not fully understood. Females produce clutches of two to six eggs (Bush *et al*. 2010), with hatchlings captured in late summer and autumn suggesting that eggs are laid in late spring to early summer (Shine 1984; How & Shine 1993; Strahan *et al*. 1998). There are no estimates for population trends or lifespan.

Neelaps calonotos feeds exclusively on small fossorial skinks, such as *Aprasia* and *Lerista* spp., which contrasts with other fossorial elapids that consume a broader and less specific assortment of prey species (Shine 1984; Strahan *et al.* 1998). Reflecting the species' specialised diet is its habitat requirements, preferring *Banksia* woodlands atop soft calcareous sand and, to a lesser extent, coastal heathlands and shrublands (Bush *et al*. 2010; Wilson & Swan 2013). Although relatively abundant in both habitats, How & Shine (1993) recorded higher capture rates of *N. calonotos* in *Banksia* woodlands, which are also the preferred habitat for skinks.

Within the Perth region, the majority of records of *N. calonotos* are from coastal locations, whereas the easternmost reports are from Forrestdale Lake Nature Reserve, Ellenbrook and Melaleuca Park (How & Dell 1994; Maryan *et al*. 2002; Glen Gaikhorst, unpublished data; Appendix 1). As with most other fossorial elapids, *N. calonotos* is absent in the Darling Range, where suitable habitat is scarce and coarse heavy soils prevent the species from efficient burrowing.

Neelaps calonotos is rarely found in small urban bushland remnants—many older records from such locations probably represent now-extinct populations, attributed to the species' preference for mature and fire-resistant habitats (Valentine *et al*. 2012). Smaller bushland remnants are more susceptible to weed infestation, bushfires and predation by feral species (Maryan *et al*. 2015; Gaikhorst *et al*. 2018) with weeds having an adverse effect, which can be amplified by bushfires, on the composition of microhabitats required by fossorial species.

DISTRIBUTION WITHIN THE PERTH REGION

Recent records indicate that *N. calonotos* is more abundant north of the Swan River (Fig. 2), particularly in heathland habitats next to the coast, as well as large undisturbed reserves of *Banksia* woodland farther inland (Arnold *et al*. 1991; How & Shine 1993; Maryan *et al*. 2002). Although the threat of urban development remains in this region, some suitable habitats for the species remain relatively intact, most notably the large expanse of *Banksia* woodland that is relatively continuous between Ellenbrook and Yeal where *N. calonotos* has been recorded (Arnold *et al*. 1991; How & Dell 1994; Maryan *et al*. 2002; Robert Audcent, pers. obs). Though the species prefers *Banksia* woodlands, it is most abundant in the extensive coastal heathlands in reserves north of Alkimos (Glen Gaikhorst, pers. comm., August 2020; Brad Maryan, pers. comm., August 2021). Unfortunately, widespread clearing of this region is planned, threatening to extirpate

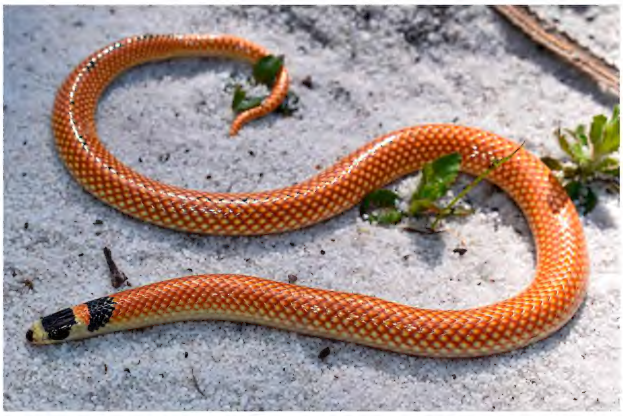

Figure 1. *Neelaps calonotos* from Whiteman Park, WA; approximately 25 cm long.

these populations. Beyond the Perth region, *N. calonotos* is considerably more abundant in the vast, undisturbed coastal heathland that extends north to Lancelin, and in an outlying population near Port Denison 300 km north of Perth (Storr *et al.* 2002; Euan Kettle, pers. comm. 2020).

South of the Swan River, in contrast, recent records of *N. calonotos* are scarcer and originate from larger inland reserves such as around Jandakot Airport and Forrestdale Lake Nature Reserve, as well as coastal heathland between Peron and Mandurah (Bamford Consulting Ecologists 2003; GHD Pty Ltd 2014, 2018; Glen Gaikhorst, pers. comm., August 2021; Brad Maryan, pers. comm., August 2021). Whereas little to no suitable habitat remains in these areas due to urban development, there are some older records from reserves where suitable habitat remains, such as Cooloongup Lake, Woodman Point Regional Park and Naval Base (Department of Biodiversity, Conservation and Attractions 2021), warranting further surveys to confirm the species' continued presence.

The southernmost limit of *N. calonotos*'s distribution is typically cited as Mandurah (Storr *et* al. 2002; Wilson & Swan 2013; Gaikhorst *et al.* 2018); however, suitable habitat is now scarce in this region, and it is likely that the Mandurah records represent a now-extirpated population (Gaikhorst *et al.* 2018). A 2009 record from Dawesville, south of Mandurah, currently marks the species' southernmost limit (Department of Biodiversity, Conservation and Attractions 2021).

DISCUSSION

Detecting *N. calonotos* can be a problematic and laborious task, as is common with other small burrowing reptiles that are rarely observed in situ. Pitfall trapping is the most frequently employed method used to survey for small vertebrate fauna, although it has its limitations, especially when it is the sole survey method. During their 11-year pitfall trapping study across 34 locations around Perth, How & Dell (2000) found that capture rates for all five fossorial elapids were relatively low. Other species often were not detected for several years, underpinning the limitations of pitfall trapping and stressing the importance of supplementary search methods, especially when surveys are time constrained, such as those preceding land clearing. Although actively

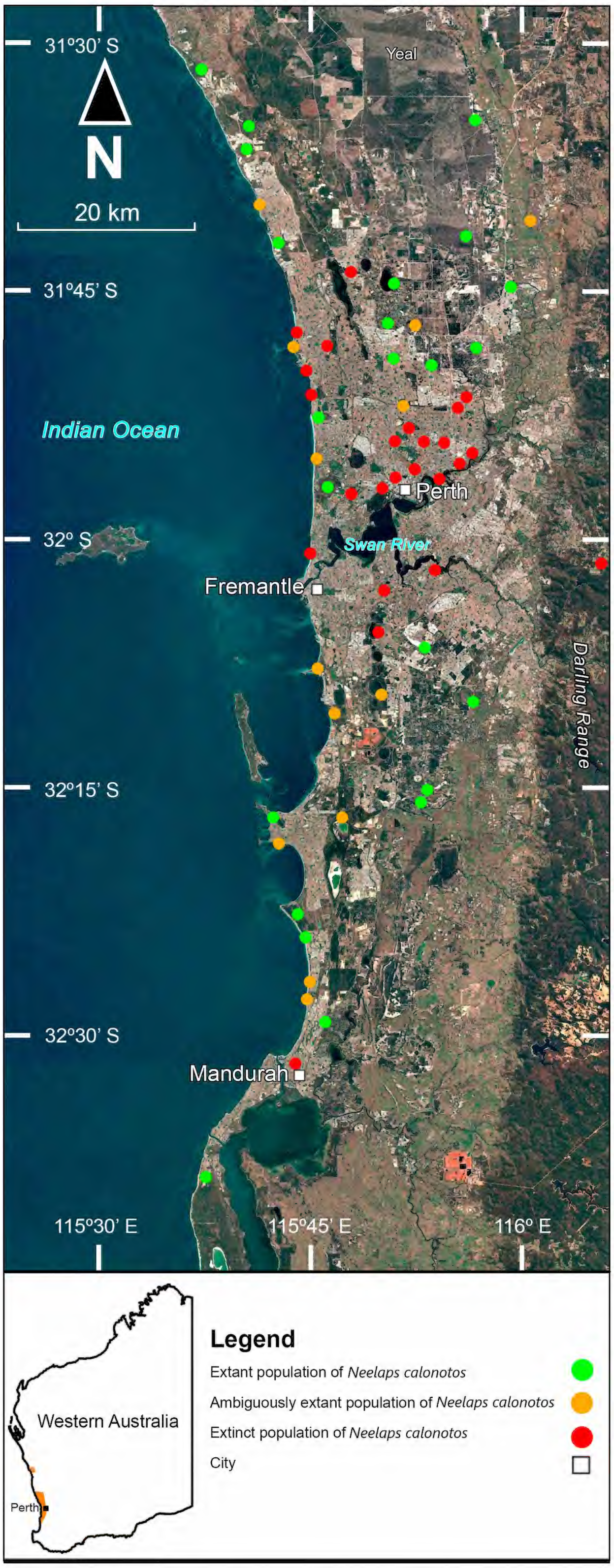

Figure 2. *Neelaps calonotos* populations within the Perth region. Green circles denote likely extant populations confirmed by records after 1990; orange circles, possibly extant populations with records predating 1990, where suitable habitat remains but where further surveying is required to confirm their presence; and red circles indicate populations that are likely extirpated due to urbanisation and land clearing. The species' overall distribution is shown in orange on the inset map. Sources for localities are summarized in Appendix 1.

searching habitats is more laborious, it is also less time-consuming as it relies less on the movement of target species, whereas passive methods such as pitfall trapping are less likely to locate seasonally inactive species. A popular method among both professional and amateur herpetologists is to use a pronged cultivator to rake through spoil heaps, soil mounds and leaf litter, beneath which fossorial reptiles seek shelter (Bush *et al.* 2007; Cogger 2014). This method is particularly productive during cooler months, when most reptiles exhibit decreased levels of activity.

Neelaps calonotos is evidently more abundant north of the Swan River, whereas records are comparatively scarcer to the south. This aspect of its distribution also applies to the four other burrowing elapids in the region of which the Jan's Banded Snake *Simoselaps bertholdi* is the most abundant. This species persists in extremely small bushland remnants north of the river (How & Shine 1993), but is scarce between Perth and Mandurah, even in larger bushland reserves. By comparison, the Narrow-banded Shovelnose Snake *Brachyurophis fasciolatus fasciolatus* is completely absent south of the river, with only two historical records suggesting its previous presence there (Department of Biodiversity, Conservation and Attractions 2021). This may be attributed to more widespread historical urban development south of the river where expansive industrial, residential and agricultural complexes replaced, and thereby destroyed, degraded or fragmented, formerly large bushland reserves. The largest remaining bushland reserves consist primarily of large swamps and lakes, such as the Beeliar Wetlands, which are ill suited for fossorial species such as *N. calonotos* and susceptible to heavy pollution due to their proximity to urbanised areas (Department of Conservation and Land Management 2006). In contrast, although urban development is rapidly consuming large bushland remnants north of the river, sizeable expanses of habitat remain intact and protected, such as Trigg Bushland, Melaleuca Park, Whiteman Park and Yanchep National Park, which are recognised for their conservation significance and accordingly protected from development.

With new populations of *N. calonotos* being discovered as a result of recent surveys (GHD Pty Ltd 2014; Glen Gaikhorst, pers. comm. 2020), it is pertinent that surveys should continue, particularly in reserves that have not been extensively investigated recently, such as Naval Base, Leda Nature Reserve, Lakelands and the southernmost network of reserves within Jandakot Regional Park. Regrettably, recent land clearing around Eglinton and Alkimos has destroyed or fragmented bushland where *N. calonotos* was recorded as locally abundant (Glen Gaikhorst, pers. comm., August 2020; Brad Maryan, pers. comm., August 2021), calling into question the value of the species' conservation status to government agencies. Nevertheless, if the species is to be conserved, it is crucial that new extensive and targeted surveys are undertaken to better understand its true extent within the Perth region.

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Appendix 1. All locations within the Perth region where *Neelaps calonotos* has been recorded based on archives from the Western Australian Museum (WAM), and published and unpublished sources, including the year of the most recent record and the current status of each population. Records after 1990 are considered 'Extant', whereas those predating 1990 are considered 'Ambiguous', if from a suitable habitat, although further surveys may be needed to confirm this. In areas where records predate 1990, and where little or no suitable habitat remains, it is highly likely that the species is now extirpated.

Location name	Latitude & Longitude	Most recent record	Reference/source	Status
Alkimos	31°37′55″S, 115°40′21″E	1998	Glen Gaikhorst, pers. obs.	Extant
Badgerup Lake	31°46′59″S, 115°50′27″E	2015	Thompson (2015)	Extant
Ballajura	31°49′34″S, 115°53′41″E	2005	Brad Maryan, pers. obs.	Extant
Banksia Conservation Reserve	32°15′54″S, 115°52′54″E	2013	GHD Pty Ltd (2014)	Extant
Bassendean	31°54′00″S, 115°57′00″E	1947	Western Australian Museum (R9228)	Extinct
Bateman	32°02′56″S, 115°50′02″E	1979	Western Australian Museum (R62170)	Extinct
Bayswater	31°55′00″S, 115°54′00″E	1950	Western Australian Museum (R9762)	Extinct
Bedford	31°54′26″S, 115°53′28″E	1951	Western Australian Museum (R10154)	Extinct
Beechboro	31°52′00″S, 115°56′00″E	1916	Western Australian Museum (R555)	Extinct
Bibra Lake	32°05′40″S, 115°49′52″E	unknown	Emerge Associates (2015)	Extinct
Bickley	32°00′21″S, 116°05′29″E	1931	Western Australian Museum (R3827)	Extinct
Bold Park	31°56′48″S, 115°45′49″E	1994	How (1998)	Extant
Casuarina	32°15′15″S, 115°53′19″E	2014	Brad Maryan, pers. obs.	Extant
Caversham	31°51′54″S, 115°57′49″E	1936	Western Australian Museum (R5940)	Extinct
Cooloongup Lake	32°17′00″S, 115°47′00″E	1968	Western Australian Museum (R9311)	Ambiguous
Cottesloe	31°59′00″S, 115°45′00″E	1930	Western Australian Museum (R3736)	Extinct
Dawesville	32°38′41″S, 115°37′36″E	2009	Department of Biodiversity, Conservation and Attractions (2021)	Extant
Dianella	31°53′00″S, 115°52′00″E	1969	Western Australian Museum (R34376)	Extinct
Eglinton	31°35′00″S, 115°40′47″E	2020	Brad Maryan, pers. obs.	Extant
Ellenbrook	31°44′42″S, 115°59′04″E	2020	Brad Maryan, pers. obs.	Extant
Embleton	31°54′00″S, 115°54′00″E	1962	Western Australian Museum (R16911)	Extinct
Forrestdale Lake Nature Reserve	32°09′53″S, 115°56′40″E	2020	Brad Maryan, pers. obs.	Extant
Gnangara Lake	31°47′11″S, 115°52′38″E	1983	Western Australian Museum (R88057)	Ambiguous
Inglewood	31°55′09″S, 115°53′10″E	1952	Western Australian Museum (R10598)	Extinct
Jandabup Lake	31°44′24″S, 115°51′21″E	2017	Department of Biodiversity, Conservation and Attractions (2021)	Extant
Jandakot Airport	32°06′30″S, 115°53′08″E	2002	Bamford Consulting Ecologists (2003)	Extant
Landsdale Park Conservation Reserve	31°49′09″S, 115°51′01″E	1994	How & Dell (1993)	Extant
Leederville	31°56′00″S, 115°50′00″E	1923	Western Australian Museum (R967)	Extinct
Madora Bay	32°28′00″S, 115°45′00″E	1977	Western Australian Museum (R30048)	Ambiguous
Mandurah	32°32′23″S, 115°44′25″E	unknown	Wilson & Swan (2013)	Extinct
Maylands	31°56′00″S, 115°54′00″E	1949	Western Australian Museum (R9558)	Extinct
Melaleuca	31°41′54″S, 115°56′30″E	2012	Department of Biodiversity, Conservation and Attractions (2021)	Extant
Mirrabooka*	31°51′46″S, 115°51′40″E	2012	Department of Biodiversity, Conservation and Attractions (2021)	Ambiguous
Mount Lawley	31°56′00″S, 115°52′00″E	1965	Western Australian Museum (R25362)	Extinct
Muchea	31°35′01″S, 115°57′00″E	1999	Department of Biodiversity, Conservation and Attractions (2021)	Extant
Mullaloo	31°46′48″S, 115°44′00″E	1978	Western Australian Museum (R61769)	Extinct
Naval Base	32°10′40″S, 115°46′46″E	1968	Western Australian Museum (R12312)	Ambiguous
North Beach	31°51′40″S, 115°45′10″E	1959	Western Australian Museum (R13324)	Extinct
Padbury	31°49′00″S, 115°46′00″E	1986	Western Australian Museum (R96383)	Extinct
Parklands	32°29′11″S, 115°46′00″E	2011	Department of Biodiversity, Conservation and Attractions (2021)	Extant

Appendix 1 (cont.)

Location name	**Latitude & Longitude**	**Most recent record**	**Reference/source**	**Status**
Pearce	31°40′44″S, 116°00′34″E	1960	Western Australian Museum (R13439)	Ambiguous
Peron	32°16′57″S, 115°42′19″E	2014	Brad Maryan, pers. obs.	Extant
Port Kennedy Scientific Park	32°22′34″S, 115°44′00″E	2012	Brad Maryan, pers. obs.	Extant
Quinns Rocks	31°41′00″S, 115°42′00″E	1967	Western Australian Museum (R29017)	Ambiguous
Riverton	32°02′00″S, 115°53′00″E	1958	Western Australian Museum (R12720)	Extinct
Safety Bay	32°18′19″S, 115°42′45″E	1968	Western Australian Museum (R6888)	Ambiguous
Scarborough	31°53′00″S, 115°46′00″E	1970	Western Australian Museum (R36158)	Ambiguous
Secret Harbour	32°23′57″S, 115°44′35″E	2019	Anonymous pers. obs.	Extant
Shenton Park	31°56′59″S, 115°48′06″E	1936	Western Australian Museum (R6054)	Extinct
Singleton	32°27′00″S, 115°45′00″E	1977	Western Australian Museum (R62263)	Ambiguous
Sorrento	31°49′00″S, 115°45′00″E	1971	Western Australian Museum (R40287)	Extinct
Tamala Park	31°42′06″S, 115°42′31″E	2015	Brad Maryan, pers. obs.	Extant
Trigg Bushland	31°52′42″S, 115°45′18″E	1995	How & Dell (1993)	Extant
Wanneroo	31°45′00″S, 115°48′00″E	1982	Western Australian Museum (R81980)	Extinct
West Perth	31°57′00″S, 115°50′00″E	1947	Western Australian Museum (R9176)	Extinct
Whiteman Park	31°48′16″S, 115°56′52″E	2021	pers. obs. 2021	Extant
Whitfords Beach	31°48′23″S, 115°43′45″E	1971	Western Australian Museum (R25065)	Ambiguous
Woodman Point Regional Park	32°07′53″S, 115°45′33″E	1965	Western Australian Museum (R25065)	Ambiguous
Yanchep	31°32′01″S, 115°38′47″E	2005	ATA Environmental (2007)	Extant
Yokine	31°54′00″S, 115°51′00″E	1954	Western Australian Museum (R11264)	Extinct

* This relatively recent record is from a private property rather than a reserve; although unconfirmed, *N. calonotos* may be present in nearby bushland remnants.

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One biodiversity hotspot to rule them all: southwestern Australia—an extraordinary evolutionary centre for plant functional and taxonomic diversity

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Abstract

The Southwest Australian Floristic Region (SWAFR) is a global biodiversity hotspot with exceptional plant species richness, endemism and rarity linked to ancient landscapes, extremely infertile soils, complex habitats and a relatively stable climatic history. It contains about 9000 plant taxa (~8000 species), the majority of which are endemic. Key functional traits for nutrition, fire and pollination were assigned to 77% of taxa and extrapolated for all genera using existing data sources and new observations. Plants with complex mineral nutrition traits are 3–14 times more abundant than global averages, including 18% of all known ectomycorrhizal plants, 40% of nonmycorrhizal plants with cluster roots, 18% of carnivorous plants and most *Thysanotus* species with unique mycorrhizas. Many SWAFR plants also have complex pollination relationships with specific insects (30%), birds (12%), or non-flying mammals (2%). Most also have single (90%) or multiple (48%) traits that are important for fire survival and recovery, such as soil seed banks (70%), canopy-stored seed (20%), resprouting (24%), fire-promoted germination (56%), enhanced flowering (33%), or fire avoidance (14%). Despite these adaptations, fire impacts can cause substantially altered plant diversity and dominance, loss of species, seed banks that take decades to recover, and increased presence of weeds. Most SWAFR plants have adaptive traits for nutrition, pollination and fire, with the most complex trait combinations in specific families and genera that also are the most taxonomically diverse in this biome. Trait variability within genera or even species reveals that strong selective pressures are still driving local adaptation. Species richness patterns of highly diverse trait-complex clades extend the SWAFR boundary into the interzone where ironstone ranges, shrublands and eucalypt woodlands include additional local hotspots for plant diversity and endemism.

The SWAFR is globally unique due to the high proportion of plants with exceptionally complex functional traits that have evolved over long periods in response to adverse conditions, thereby making this region a key plant diversity hotspot for trait evolution. The SWAFR is the best location globally for studying long-term impacts of climate and soil conditions on plant functional and taxonomic diversity, and provides a preview of future conditions elsewhere. However, plants in this region now face even more severe fires, droughts, pollinator shortages and declining soil health. This greatly increases the need for well-resourced and science-based adaptive approaches for ecosystem management and rare flora conservation.

Keywords: southwestern Australia, biodiversity hotspot, mycorrhizas, plant nutrition, pollination, adaptation to fire, trait evolution

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INTRODUCTION

The Southwest Australian Floristic Region (SWAFR) encompasses an area with a predominantly Mediterranean climate bounded by semiarid regions. It is one of the 25 original biodiversity hotspots for species richness and endemism (Myers *et al*. 2000). Using its original boundaries, the region contains over 7000 plant species of which 52% are endemic, whereas a similar sized area in eastern Australia contained 4810 species, but only 14% were endemic to that region (Thiele & Prober 2014). Within the SWAFR there are 363 threatened, six presumed extinct and 2074 apparently rare (priority flora) plants (florabase.dpaw.wa.gov.au, accessed 30-4-21) and landscape age is positively correlated with the local diversity of rare flora species (Gosper *et al.* 2021a). Smaller biodiversity hotspots for specific groups of organisms have also been recognised in Australia for *Acacia* (González-Orozco *et al*. 2013), eucalypts (González-Orozco *et al*. 2014) and orchids (Phillips *et al*. 2011). The SWAFR contains five of the 15 recognised national biodiversity hotspots (www.wildlifelandtrust.org.au, accessed 30-4-21), as well as 14 additional areas of exceptionally high plant endemism and species richness missing from the national list (Hammer *et al*. 2018). Important threats to plant diversity in this region include vegetation clearing and fragmentation, substantial declines and fluctuations in rainfall, contraction of the Mediterranean climate zone, increasing frequency and severity of fires, *Phytophthora* dieback disease,

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weed invasion and feral animals (O'Donnell *et al.* 2018; Hoffmann *et al.* 2019; Cross *et al.* 2020; Bergstrom *et al.* 2021; Ritchie *et al.* 2021; Gosper *et al.* 2021b).

The most important factors regulating global plant diversity include the size of bioregions, dominance by intermediate sized plants, complex environmental gradients and moderate disturbance regimes (Keddy 2005). In addition, ancient landscapes with relatively stable climates (OCBILs) and long periods without major disturbance can provide the opportunity for plants to maintain exceptionally high diversity (Cowling *et al.* 1994; Hopper & Gioia 2004; Mucina & Wardell-Johnson *et al.* 2007). In these areas weathering and erosion increase soil and regolith complexity, whereas prolonged leaching leads to extremely low soil fertility (Verboom & Pate 2015; Zemunik *et al.* 2016). Studies in Australia and elsewhere have confirmed that species richness is typically greatest at nutrient poor sites (Beadle 1954; Specht & Rundel 1990; Lambers *et al.* 2010). For example, shrublands and woodlands in southwestern Australia have more plant species in a 100 m^2 plot compared to soils with higher levels of phosphorus and nitrogen (Gibson *et al.* 2004; Zemunik *et al.* 2016). The SWAFR has a large proportion of species that are specialized and adapted to the low-nutrient soils that predominate in this highly weathered landscape (Hopper & Gioia 2004; Lambers *et al.* 2010). Even areas with redistributed substrates are comparatively ancient by global standards (Brundrett *et al.* 2017).

In Australia, vegetation patterns are also strongly driven by landform complexity and hydrology (Fordyce *et al.* 2007; Cardillo & Pratt 2013; Reyes *et al.* 2015; Brundrett *et al.* 2017). This complexity may be partly driven by the plants themselves, because cumulative long-term effects of root exudates on soil minerals are linked to laterite or clay formation (Pate & Verboom 2009). Complex landscapes also lead to edaphic specialisation by plants and provide refugia against extinction (Verboom & Pate 2015; Brundrett *et al.* 2017). These specialised habitats include saline areas, rock outcrops, banded ironstone ranges and wetlands (Mucina & Wardell-Johnson 2007; Pate & Verboom 2009; Macintyre & Mucina 2021). High species richness in this region is also linked to steep climatic gradients (Bui *et al.* 2014; Cook *et al.* 2015; Jones *et al.* 2016) and effective adaptations to survive severe droughts and fires (Orians & Milewski 2007; Carpenter *et al.* 2015; Groom & Lamont 2015). Thus, vegetation patterns, which are complex in areas of high plant diversity in Australia, are the product of the feedback processes shown in Figure 1 in addition to plant competition over evolutionary timescales.

Although the nature of trait evolution can be controversial in some cases (e.g. Bradshaw *et al.* 2011), there is compelling evidence that the evolution of traits for nutrition, fire and pollination have been driven by strong habitat specific selective pressures in the SWAFR. For nutrition traits this evidence includes strong correlations between soil nutrient status and the dominance and diversity of more specialised plants, as explained below in **Pollination traits**. There also are many SWAFR plant clades with advanced pollination strategies that have relatively specific pollen vectors and complex floral structures, which are also known as syndromes (e.g. Keighery 1980; Brown *et al.* 1997; Toon *et al.* 2014). For fire traits this evidence includes many plants, descended from fire intolerant ancestors, which have acquired traits that enhance fire survival. These include members of the Proteaceae, Myrtaceae, Restionaceae and Fabaceae, for which increased dominance of fire tolerant species over time in Australia is well documented in the fossil record and phylogenetic studies (Lamont *et al.* 2019). The fire intolerance of many rainforest plants limits the extent of this vegetation type in Australia, yielding 'islands of green in a sea of fire' (Bowman 2000). Lamont *et al.* (2019) identify fire as an important evolutionary trigger that led to multiple fire traits, some of which evolved as early as the Cretaceous in response to increased fire intensity or frequency and others that arose later to enhance the post-fire success of plants.

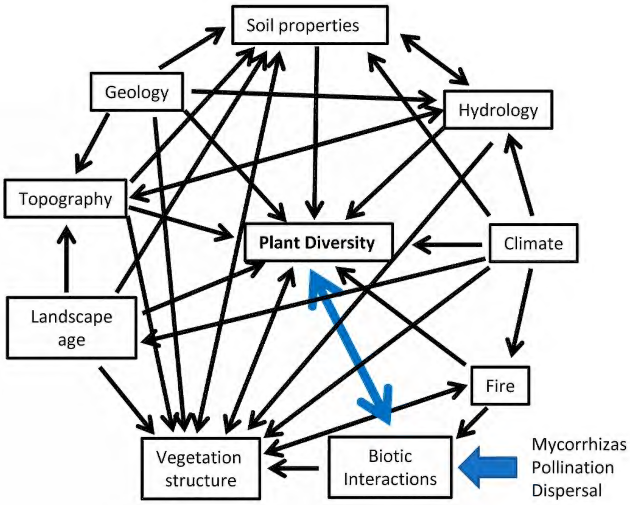

Figure 1. Interacting environmental actors that act as selective pressures in the SWAFR (after Brundrett *et al.* 2017).

Mycorrhizal association types are normally consistent within plant families (Trappe 1987; Brundrett & Tedersoo 2018; Brundrett 2021). Most of the globe is dominated by families that have consistent arbuscular mycorrhizas (AM), an association that arose with the first land plants, along with ectomycorrhizal (EM) and nonmycorrhizal (NM) plants that diverged from AM plants in the Cretaceous (Brundrett & Tedersoo 2018; Soudzilovskaia *et al.* 2019). Australia also has many plant families in which ancestral traits have remained consistent, but a global comparison of mycorrhizal associations reveals that exceptions to this are more common in Australia, and are especially prevalent in the southwest of Western Australia (Brundrett 2017a). This is largely due to two large plant families—the Fabaceae and Myrtaceae—that have exceptionally variable root traits, (AM, EM and AM, or cluster roots with or without loss of mycorrhizas). The SWAFR is a globally significant region for root evolution, and also has many carnivorous plants and nitrogen fixing species (Lambers *et al.* 2010; Brundrett & Tedersoo 2018; Cross 2020). Species that grow in this region are also exceptionally efficient at utilising and recycling nutrients (Hayes *et al.* 2014). Furthermore, this area has an exceptional diversity of plants with complex floral traits linked to relatively specific or extremely specific pollinators (Brown *et al.* 1997; Brundrett, Ladd & Keighery unpublished data).

Bushfires in Australia have substantiality increased in frequency, intensity and size in recent years (Godfree *et al.* 2021), with the Southwest being burnt more often than arid areas (Miller & Murphy 2017). Traits that lead to increased survival or reproduction of plants after severe fire have been important in Australia and globally since the Cretaceous (Pausas *et al.* 2004; Crisp *et al.* 2011; Lamont & He 2017; Bond 2015). The most common fire traits in Western Australia are canopy-stored seed (serotiny), vigorous resprouting, long-lived soil seed banks and promotion of seed germination by fire (Miller & Dixon 2014; Groom & Lamont 2015; Brundrett & Longman 2016; Ald & Ooi 2017; Pausas *et al.* 2018). Other plant traits common in the SWAFR flora include xerophily, assisted seed dispersal and groundwater dependence (Zencich *et al.* 2002; Groom & Lamont 2015). However, these traits are globally widespread, so are less useful for designating hotspots of plant evolution.

This paper summarises knowledge of nutrition, pollination and fire traits of plants in the southwest Australian biodiversity hotspot by addressing the following objectives:

1. Compile data on relatively specialised traits for mineral nutrition, pollination and fire for SWAFR plant species.
2. Compare the taxonomic diversity of plants with specific traits or combinations of traits in the region to global averages.
3. Identify families and genera which exhibit exceptional trait variability and/or have the most highly specialised combinations of traits in multiple categories.
4. For clades identified in objective 3, compare their taxonomic diversity and taxonomic complexity (unnamed or subspecies taxa) relative to other clades.
5. Compare geographic diversity patterns of selected highly specialised clades to existing or proposed boundaries to the SWAFR bioregion.

METHODS

Study area and species

The Southwest Australian Floristic Region boundary used here is loosely based on the southwest phytogeographical region, as defined by Ebach *et al.* (2015), which is substantially larger than the original SWAFR boundary (Gioia & Hopper 2017), but generally corresponds to the boundary between the Eremaean Province and the South-Western Interzone on the vegetation map of Western Australia (Beard *et al.* 2013). As defined here SWAFR includes nine IBRA7 regions—Avon Wheatbelt, Coolgardie, Esperance Plains, Geraldton Sandplains, Jarrah Forest, Mallee, Swan Coastal Plain, Warren and Yalgoo—totalling about 480 000 km^2, (Fig. 2). Species occurrence data for these bioregions was obtained from the Australian Virtual Herbarium for the SWAFR and the entire State (avh.chah.org.au, accessed 21-1-2021). The West Australian Herbarium database (florabase.dpaw.wa.gov.au) was subsequently used to check and update these lists, which were edited to remove records of weeds, cultivated native plants, non-terminal taxa, hybrids and invalid names. Taxonomic complexity was calculated using subspecies (including varieties or forma) and informal phrase names within families (Appendix 1).

Definition and quantification of traits

In this study specialised traits were defined as those absent from the ancestors of plants and also missing, or substantially less frequent, in plants from most other biomes. Plants were allocated to mineral nutritional trait categories by compiling lists of host and non-host plants using the data sources listed in Table 1. These categories include nutritional traits that were variable within families, as well as carnivorous, parasitic and nitrogen

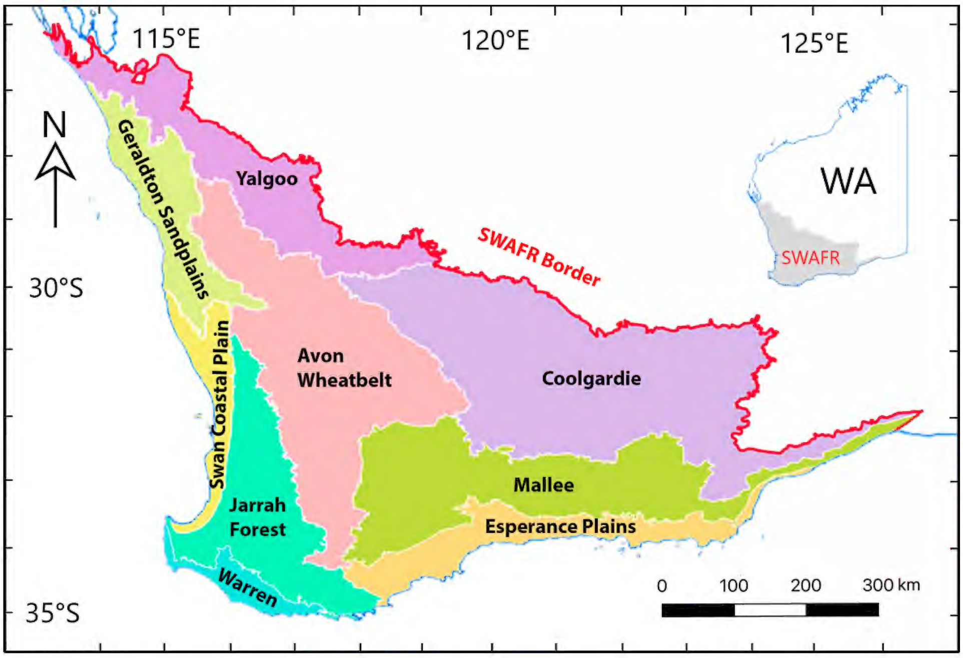

Figure 2. The Southwest Australian Floristic Region as defined here relative to IBRA regions in Western Australia (www.environment.gov.au/land/nrs/science/ibra).

fixing plants. This modified dataset for the SWAFR (Fig. 2) was also compared with state-wide, Australian and global totals for the same traits calculated by Brundrett (2017a, b) and Brundrett & Tedersoo (2018). These records are available in the FungalRoot database (Soudzilovskaia *et al.* 2020).

Data from a separate project that compiled existing data for SWAFR plants, provided the diversity of plants with specialised pollination mechanisms and/or extremely specific pollinators (Brundrett, Ladd & Keighery unpublished data). These syndromes, which are defined by flower forms and pollinator records, include bird or animal pollination, secondary pollen presentation, deception and specific associations with insects, are listed along with key references in Table 1.

Records of fire traits such as lignotuber presence, resprouting capacity and canopy stored seed are available for many Western Australian species within species descriptions in the taxonomic literature (Table 1), including the Flora of Australia online (www.ausflora.org.au). Taxon-specific data were also obtained from 52 other studies (Table 1), including earlier compilations by Bell *et al.* (1993), Burrows *et al.* (2008), Enright *et al.* (2014), Clarke *et al.* (2015) and Tsakalos *et al.* (2019).

Table 1. Trait types, abbreviations and major sources of information.

Abbreviation	Trait type	Key references
Plant nutrition, root types and habitats		
AM	Arbuscular mycorrhizas	Australian data: updated from Brundrett (2008, 2017a);
EM	Ectomycorrhizas (primarily)	Ectomycorrhizal hosts: Tedersoo & Brundrett (2017);
EM-AM, etc.	Dual mycorrhizas (2 types)	Global data: Brundrett (2017b);
Eric	Mycorrhizas in Ericaceae	Flowering plant species: Christenhusz & Byng (2016);
Orchid	Mycorrhizas in Orchidaceae	Parasitic plants: Nickrent (2020);
Thys	Mycorrhizas in Thysanotus spp.	Carnivorous plants: Cross *et al.* (2020);
NM	Nonmycorrhizal	Australian Orchidaceae: Backhouse *et al.* (2019);
N2F	Nitrogen Fixation	Cyperaceae: Barrett (2013);
Carn	Carnivorous plant	Dauciform roots: Shane *et al.* (2005);
Para	Parasitic plant	Nitrogen fixing symbioses: Tedersoo *et al.* (2018)
CR	Cluster Roots	
DR	Dauciform Roots	
LRH	Long Root Hairs	
SBR	Sand Binding Roots	
Marine	Marine aquatic plant	
Aqua	Aquatic plant (freshwater)	
ASD	Arid, Saline and Disturbed habitats	
Pollination		
Bird	Bird Pollination	Brown *et al.* (1997);
BPB	Buzz Pollination by Bees	Brundrett (2014);
GIP	General Insect Pollination	Brundrett & Keighery unpublished data;
NFM	Non-Flying Mammal pollination	Chinnock (2007);
SD	Sexual Deception	French (2012);
SIP	Specialised Insect Pollination	French & Nicolle (2019);
SP	Self-Pollination	George (1999);
SPP	Secondary Pollen Presentation	George & Pieroni (2002);
VD	Visual Deception	Groom & Lamont (2015);
Water, Wind	Non biotic	Hopper (1993);
		Keighery (1980);
		Olde & Marriott (1995)
Fire survival or propagation		
CSB	Canopy Seed Bank	Baker *et al.* (2005); Barrett & Dixon (2001); Bell (2001); Bell *et al.*
FAA	Fire Avoidance by Annual growth	(1984, 1993, 1996); Bell & Pate (1996); BGPA (2016); Bellairs & Bell
FE	Fire Ephemeral	(1990); Brown *et al.* (1998); Brundrett (2014); Brundrett *et al.* (2018,
FPF	Fire Promoted Flowering	2019, 2020); Burrows *et al.* (2008); Chinnock (2007); Clarke *et al.*
GDP	Groundwater Dependant Plant	(2007); Cochrane *et al.* (2001, 2002); Collette & Ooi ((2020);
GPF	Germination Promoted by Fire	Commander *et al.* (2009); Crisp & Cook (2003); Cross *et al.* (2020);
NSH	Non-Susceptible Habitat (e.g. halophyte, aquatic)	Enright *et al.* (2007, 2014); French (2012); French & Nicolle (2019);
RAG	Resprouts Above Ground	Froend & Sommer (2010); George (1999); George & Pieroni (2002);
RCB	Resprouting from Corm or Bulb	Gosper *et al.* (2019); Grant & Koch (1997); Groom & Lamont
RLR	Resprouts from Lignotubers, roots, or Rhizomes	(2015); Hidayati *et al.* (2012); Hopper (1993); Lamont & Downes
SAF	Short-lived After Fire	(2011); Meney *et al.* (1994); Meney & Pate (1999); Olde & Marriott
SGP	Seed Germination Promoted by fire	(1995); Pate & Dixon (1982); Pate *et al.* (1985, 1991); Roche *et al.*
SIm	Severely Impacted by fire	(1997); Rokich *et al.* (2000); Stevens *et al.* (2016); Tieu *et al.* (2001);
SSB	Soil Seed Bank	Tsakalos *et al.* (2019); van der Moezel *et al.* (1987); Ward *et al.*
VFF	Highly Flammable Foliage	(1997); Wardell-Johnson *et al.* (2007); Zenich *et al.* (2002); Zhao &
WDS	Wind-Dispersed Seed (or spores)	Ladd (2014)

Data on seed banks were also obtained from restoration projects using respread topsoil in banksia woodland and kwongan (sclerophyllous shrubland) ecosystems (Table 1). By combining data sources and personal observations, the majority of plants (77%) could be directly assigned to all fire traits, or had data for some of these traits (92% in total). In cases where different trait states are reported within taxa both records are included and noted in the trait variability field. The fire-trait categories used in Table 1 are based on Groom & Lamont (2015) with additional categories for species with substantially enhanced flowering in the first 1–5 years post-fire, are short lived after fire (one year to several decades), or have topsoil-stored seed. Two categories were split (fire-enhanced seed germination and resprouting) between reported totals for traits and extrapolated totals for genera (proportion of sampled taxa with trait X total taxa in genus). Most traits were highly consistent within genera and between different data sources. Additional traits that are important in Western Australia were also noted, such as high flammability of leaves, thick bark, post-fire seed dispersal by wind and phreatophytes (plants utilising groundwater). All data are available from the author or the AusTraits database.

The taxonomic diversity of plants with different combinations of acquired traits for nutrition, pollination and fire were also determined (Appendices 1, 2). Trait complexity was assigned to a scale from zero, for ancestral states, to six, for the most advanced state. Trait categories were averaged for genera and weighted averages were calculated for families (Appendix 1). Trait variability was ranked as (1) basal traits that are highly consistent within families, (2) more variable traits that are usually consistent within genera and (3) highly variable traits that vary considerably within genera or even within species (Appendix 1). Ratios of the taxonomic diversity of plants with one or more complex traits were used to compare the SWAFR to global averages where comparable data exists. Linear regressions fit the comparative data best, explaining 24% of the variability between traits and species richness in families.

Diversity patterns for taxa with complex traits

Diversity maps were used to investigate spatial patterns in plant traits. Datasets for selected plant families or genera were analysed with Biodiverse software (Laffan *et al*. 2010) using the moving window method with 0.5° cells with and an 1° neighbouring area. Results of different diversity and endemism metrics produced similar results, so only a species richness map is presented.

RESULTS AND DISCUSSION

Overall plant diversity

An updated list of plant species for the larger SWAFR area (Fig. 2) contains 7883 species (including unnamed species with informal names) and 8703 taxa (including subspecies, varieties and forma). The overall diversity of vascular plants in all of Western Australia in January 2021 according to the data sources used was 11 415 species (12 666 taxa). Totals for families of plants in the Southwest (Appendix 1)s are substantially higher than previous estimates of the southwest floristic region (Gioia & Hopper 2017) due to recent taxonomic work (e.g. Wege & Shepherd 2020) and a 34% increase in the area now included in the region.

Despite species being named at a steady rate, over 1000 known unnamed species remain in Western Australia (Wege & Shepherd 2020). Conversations with botanists also revealed that there still are many unnamed and unlisted plants, and that many existing species encompass much wider morphological or genetic variation than would normally be accepted. Thus, the diversity of SWAFR plants is likely to exceed 10 000, about twice that estimated when the area was first recognised as a major global biodiversity hotspot (Myers *et al*. 2000).

Plant nutrition

Nutritional complexity is exceptionally high in Australia relative to global averages (Brundrett 2017a) and in the SWAFR more so than the rest of the continent (Fig. 3). There are ~1600 taxa with cluster or dauciform roots and ~2000 with EM or EM-AM roots, as well as ~3000 other NM plants. Furthermore, plants in the SWAFR show unique levels of complexity due to variability within families or even genera for some traits (see text box, *Nutritional trait complexity*). Other distinct trends include exceptional numbers of carnivorous plants (127) and marine plants (19), as well as many parasitic plants (69), all of which have NM roots (Fig. 4). The diversity of parasitic plants is relatively high for a temperate region and the presence of widespread parasitic trees such as *Nuytsia floribunda* and four species of *Santalum* is also exceptional.

Plants in families reported to have nitrogen fixing associations, which also have one or more other nutritional traits, are also highly diverse (1270) relative to global totals (~20 000, Tedersoo *et al*. 2018). Nitrogen fixation has been confirmed for some *Acacia* spp. and other Fabaceae (e.g. Hansen *et al*. 1987), *Allocasuarina*

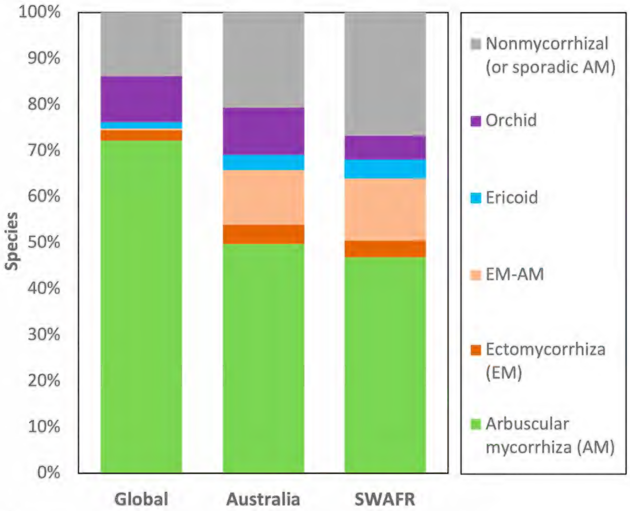

Figure 3. Relative proportions of species with different mycorrhizal association types or nonmycorrhizal roots globally, in Australia and in the Southwest. See Table 1 for data sources.

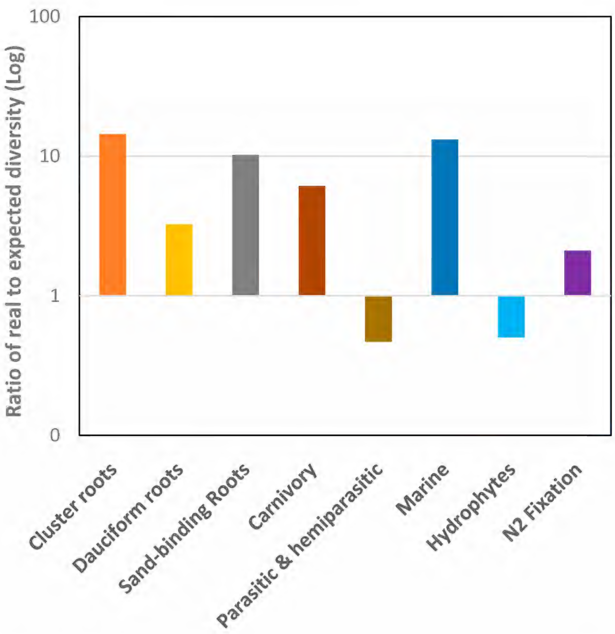

Figure 4. Relative proportions of highly specialised nonmycorrhizal, parasitic and nitrogen fixing plants in southwestern Australian taxa relative to global averages. See Table 1 for data sources.

spp. (Dawson *et al.* 1989) and coralloid roots (Fig. 5I) of the cycad *Macrozamia riedlei* (Grove *et al.* 1980). It has been assumed that all members of these families can fix nitrogen when required (Appendix 1), but it is common to find non-nodulated individuals. Members of the Zygophyllaceae have been reported to fix nitrogen (Tedersoo *et al.* 2018), but information on Australian species is lacking.

Further research is required to resolve trait complexity (see text box, *Nutritional trait complexity*). Both EM and cluster roots are considered to be more energy intensive than AM roots to produce, but these costs are compensated for by improved nutrition in highly infertile soils where phosphorus is tightly captured (Shane *et al.* 2005; Lambers *et al.* 2018). NM monocot species in certain families commonly have dauciform roots, which function like cluster roots, and sand binding roots that have less studied roles (Shane *et al.* 2005; Smith *et al.* 2011). Ectomycorrhizal roots typically also require more energy than AM roots, but are also believed to be more efficient, especially in soils high in organic matter (Raven *et al.* 2018; Soudzilovskaia *et al.* 2019; Li *et al.* 2020). Plants with advanced nutritional specialisations are typically most successful on the least fertile soils in Western Australia (Lambers *et al.* 2010; Zemunik *et al.* 2016; Brundrett *et al.* 2017a).

Australian habitats also contain an exceptionally high diversity of hypogeal (truffle-like) EM fungi (Fig. 5K), whose spores are dispersed by larger animals and insects (Bougher & Lebel 2001; Houston & Bougher 2010; Sheedy *et al.* 2016). SWAFR plant lineages with EM, including some shrubs in the Fabaceae and Myrtaceae, are keystone species for fungus feeding animals such as Gilbert's potoroo, bandicoots and woylies, as well as geotrupid beetles (Bougher & Lebel 2001; Houston & Bougher 2010; Nuske *et al.* 2017). Fungi that fruit underground in relatively dry habitats have undergone convergent evolution resulting in larger digestion-resistant spores and stronger scents to attract animals (Sheedy *et al.* 2016). Thus, animal dispersal is required for many essential symbiotic fungi, adding another layer of complexity to SWAFR ecosystems.

Nutritional trait complexity

Examples of plant clades with complex nutrition include dual AM-EM associations, cluster roots and invertebrate trapping structures (Fig. 5). The data reveals multiple switching events from arbuscular mycorrhizas (AM) to ectomycorrhizas (EM), or from AM to cluster roots, especially in the Myrtaceae and Fabaceae (Fig. 6). These represent clades with Newly acquired Complex Roots (NCR), most of which have diversified rapidly in the past 30 Ma (Brundrett 2017a; Brundrett & Tedersoo 2018). NCR genera are most common in two large families, the Myrtaceae and the Fabaceae:

1. The Myrtaceae includes (i) large shrubs or small trees like *Agonis*, *Kunzea* and *Eremaea*, in which EM roots are scarce and appear dysfunctional, (ii) shrubs and trees in *Melaleuca* in which species are either AM or EM-AM (Fig. 5BC) and (iii) *Eucalyptus*, *Corymbia* and other related trees whose roots primarily are EM, with occasional AM.
2. In the Fabaceae genus *Acacia* about half of the examined Australian species have EM (with AM) and the rest had only AM (Brundrett 2017a). Traits are correlated with plant size as EM are most common in trees and large shrubs. There are EM in at least four other Fabaceae genera (Appendix 1). *Daviesia* includes species with nonmycorrhizal cluster roots, as well as mycorrhizal species and a few that have both (Brundrett 2008, 2017a; Nge *et al.* 2020b). Several Fabaceae genera have cluster roots that are not always present (Appendix 1).

Compiling plant nutrition data for regions is usually straightforward because these traits are highly conserved within most plant lineages (Brundrett 2021). The SWAFR includes plant families for which data are complex due to highly variable or contradictory information. These primarily include the Fabaceae and Myrtaceae as explained above, but has also been reported in the Cyperaceae and Restionaceae. Nutritional trait innovation complexity in the SWAFR includes many more than expected clades with multiple traits that have overlapping functions, so some may be relic and redundant (Fig. 6, Appendix 1). These root trait gradients extend from AM only to AM (EM), AM-EM, EM-AM and EM (AM). These trait combinations, which list the dominant trait first and intermittent traits that may no longer be functional in brackets, form evolutionary sequences concluding in EM, or fully NM cluster roots. It has not been determined how habitat and climatic conditions and phylogeny interact to regulate nutrient trait switching, or if there also are instances of reversion back towards AM only roots (Brundrett 2017a). Many more plants belong to clades with a complex mycorrhizal status in the SWAFR than anywhere else, strongly suggesting that trait evolution is currently underway and may even be accelerating there (Brundrett 2017a; Brundrett & Tedersoo 2018).

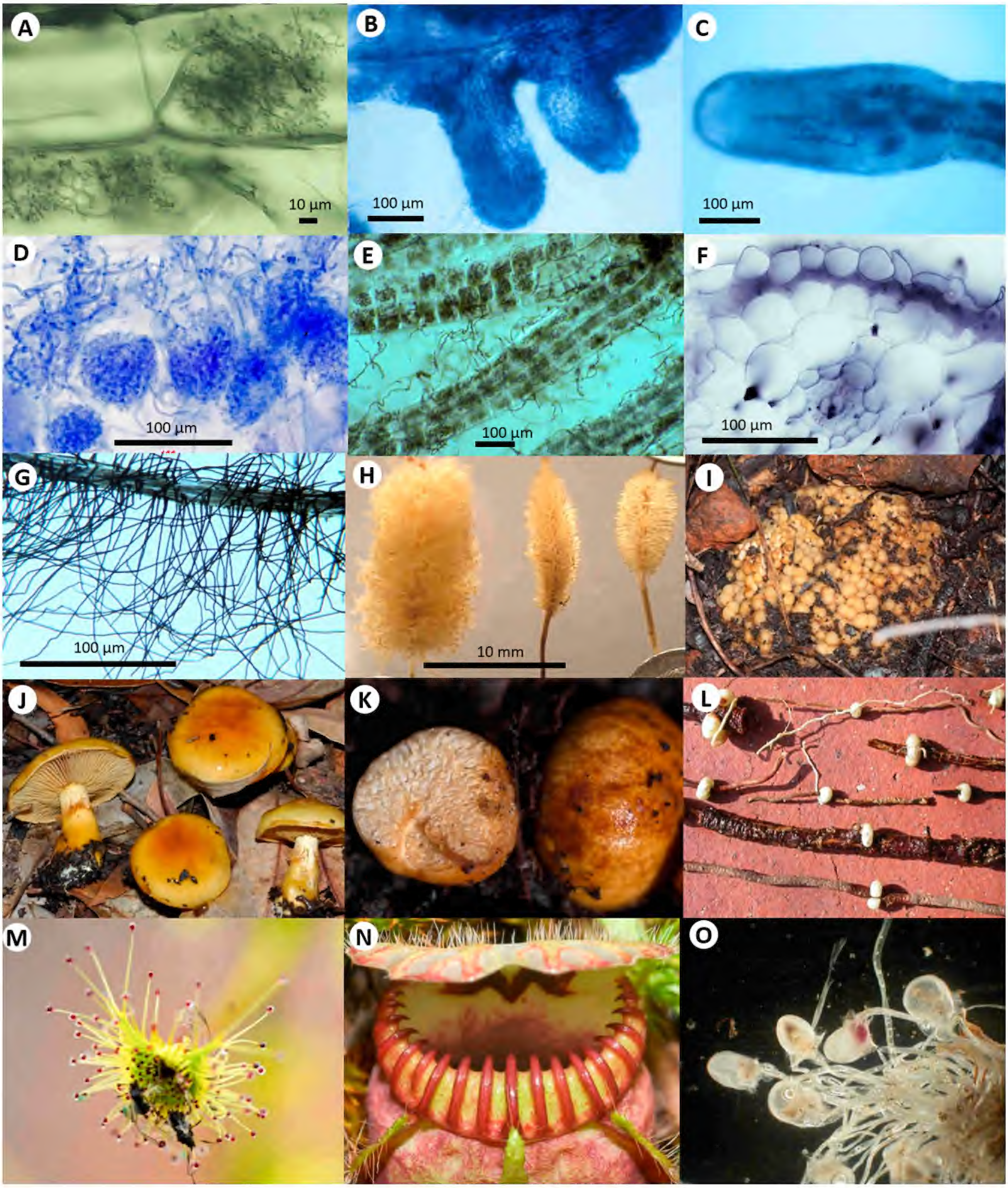

Figure 5. Examples of southwestern Australia plants with mycorrhizal root types and other highly specialised nutrient uptake mechanisms. These include: A) arbuscular mycorrhizas, B) ectomycorrhizas, or C) dual arbuscular mycorrhizas and ectomycorrhizas in *Melaleuca hamata*; D) orchid mycorrhizas in *Pterostylis sanguinea*; E) ericoid mycorrhizas in *Leucopogon verticillatus*; F) unique sub-epidermal associations of *Thysanotus*; G) long root hairs of a nonmycorrhizal carnivorous plant *Drosera erythrorhiza*; H) nonmycorrhizal cluster roots of *Hakea prostrata*; I) coralloid nitrogen-fixing roots of *Macrozamia riedlei*; J) ectomycorrhizal fungus *Cortinarius sinapicolor*; K) animal dispersed truffle-like ectomycorrhizal fungus *Zelleromyces*; L) parasitic root haustoria of *Nuytsia floribunda*; M) glandular leaf invertebrate traps of *Drosera menziesii*; N) leaf pitcher invertebrate traps of *Cephalotus follicularis*; and O) suction invertebrate traps of *Utricularia multifida*.

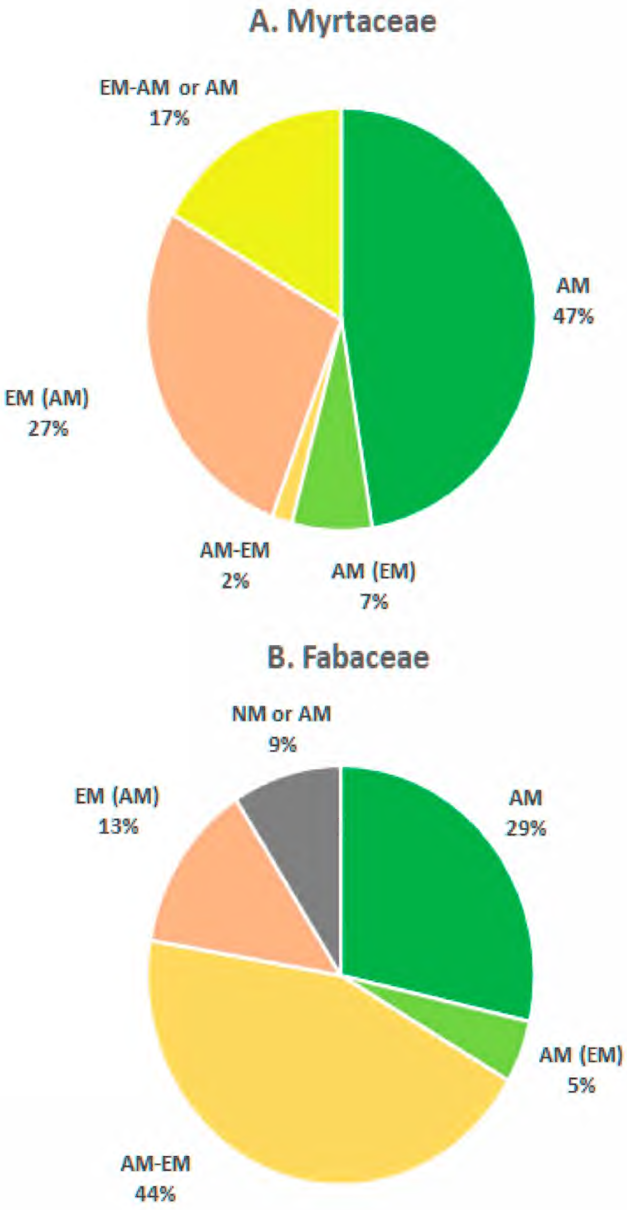

Figure 6. Case studies of families or genera with exceptionally complex nutritional traits within southwestern Australia for A) the Myrtaceae and B) Fabaceae. AM = arbuscular mycorrhizas, EM = ectomycorrhizas, NM = nonmycorrhizal.

Pollination traits

West Australian plants typically have specialised mechanisms that increase pollination efficiency and improve outcrossing (Brown *et al.* 1997; Groom & Lamont 2015; Brundrett, Ladd & Keighery unpublished). These include relatively or extremely complex interactions with specific insects, birds and non-flying mammals (Fig. 7) such as:

1. Non-biotic pollination in 993 wind pollinated and 35 water pollinated taxa (marine plants or hydrophytes).
2. Flowers primarily or partly bird pollinated in over 1000 taxa, much more than global averages. Flowers in these plants have been modified to be more attractive and accessible to birds such as honeyeaters.
3. At least 130 taxa are pollinated by non-flying mammals, especially honey possums, which also visit many other flowers.
4. There are very specific relationships with insects in over 3500 plants that have complex flower structures including secondary pollen presentation, buzz pollination and post-pollination colour changes.
5. The most complex families include the Myrtaceae with ~130 species with bee pollinated flowers and ~100 that are primarily bird pollinated. The Fabaceae includes ~20 bird-pollinated species and ~600 with specific insect visitors (Appendix 1).
6. Extreme pollination specialisation occurs in the Orchidaceae, including >200 taxa with visually deceptive flowers that lack rewards for pollinators and >170 with highly specific insects attracted by sexual deception (Brundrett 2014).

Responses for fire

The majority of SWAFR plants (90%) have at least one acquired fire-response trait (Fig. 8), including most trees, many shrubs and other long-lived perennials with rhizomes, bulbs or corms (Appendix 1). Overall, 48% of taxa have multiple fire traits, such as enhanced seed germination along with promoted flowering and/or resprouting (Fig. 8). The data in Figure 8 includes both conservative values based on documented responses only, as well as estimates of all species likely to have such traits. Fire-response traits are highly variable in some families and genera (see text box, *Fire trait complexity*).

RESPROUTING

At least 1500 species in 67 families resprout after fire (Appendix 1). Resprouting from enlarged subterranean stem bases (lignotubers) occurs in over 1000 dicot taxa and there are 616 monocots with rhizomes that normally resprout after fire. A further 69 rhizomatous hydrophytes or marine plants avoid fire. Many trees have lignotubers, as do shrubs in the Myrtaceae and Proteaceae, but some also or only resprout from epicormic buds in their trunk and branches (Figs 9, 10). Lignotubers, stems and rhizomes are combined, as many reports do not specify how resprouting occurs (Appendix 1). Subterranean bud protection is coupled with storage organs to fuel rapid regrowth after fire (Paula *et al.* 2016). Resprouting in *Daviesia* spp. is driven by a unique type of storage roots (Pate & Dixon 1982; Crisp & Cook 2003).

Increased foliage flammability due to essential oil accumulation occurs in at least 900 resprouter species in the Myrtaceae, Rutaceae and Xanthorrhoeaceae (Fig. 9J). This trait increases local fire intensity resulting in a competitive advantage over plants that lack rapid regrowth after fires (Bond & Midgely 1995; Bowman *et al.* 2014), but can also lead to high mortality after extreme fires.

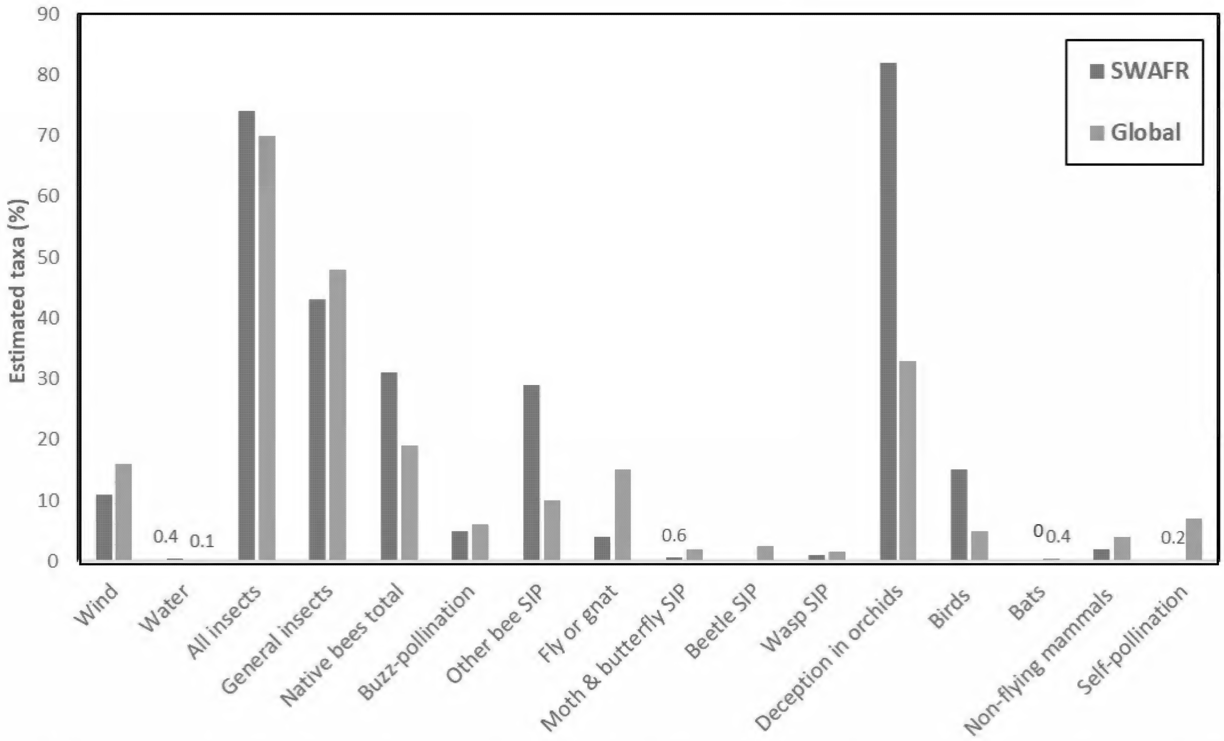

Figure 7. Summary of pollination traits in southwestern Australian plants relative to published estimates of global averages, with ferns included for comparison (SIP = specialised insect pollination). Only values <1 are provided. See Table 1 for data sources.

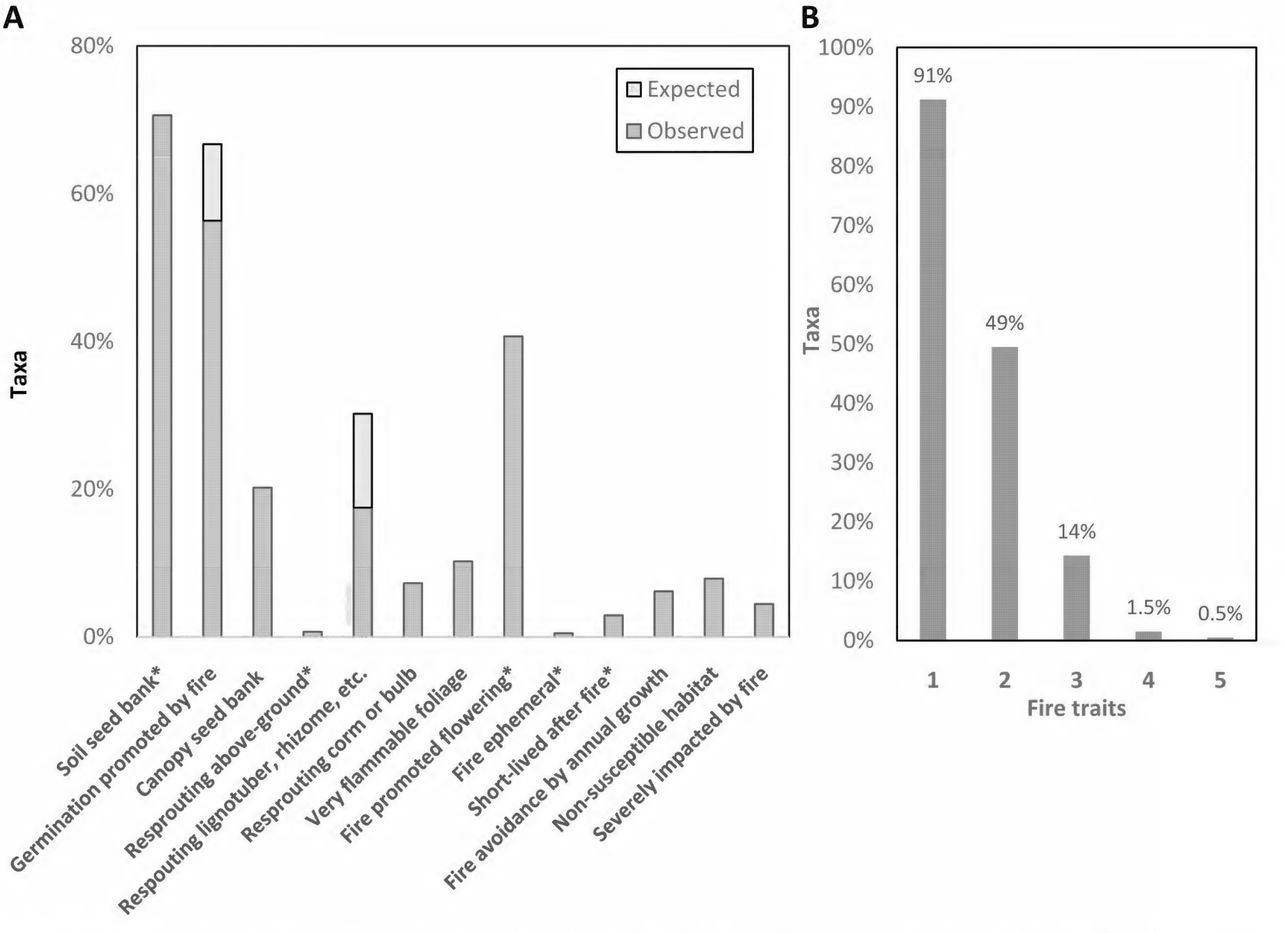

Figure 8. A. Summary of data on fire trait allocations for plant taxa in southwestern Western Australia (see Appendix 1; * indicates not a discrete category). B. The proportion of these taxa with single or multiple fire traits. Two traits with less data include extrapolated values for all taxa.

Resprouting plants are important in Mediterranean ecosystems, savannahs and prairies and can also be found in tropical or temperate forests after storm damage (Vesk & Westoby 2004; Maurin *et al*. 2014; Charles-Dominique *et al*. 2015; Pausas *et al*. 2016; Paula *et al*. 2016). The global distribution of tropical forests and savannas is strongly regulated by both rainfall and fire, as rainforests species tend to be fire intolerant (Bowman 2000; Murphy & Bowman 2012). Overall, the diversity of resprouting plants is much higher in the SWAFR than expected in most other regions. This strategy has originated many times within some genera and can even vary within species (see text box, *Fire trait complexity*). The nature of resprouting in SWAFR plants also differs from that in many other regions due to the importance of subterranean woody structures such as lignotubers and modified roots.

There are 543 geophytic species with corms or bulbs in the region (Fig. 8, Appendix 1). Many of these have vigorous growth and enhanced flowering after fire (Fig. 9O). There are at least 13 000 geophytic plants with corms, bulbs or rhizomes globally (Howard *et al*. 2019). They are common in all areas with seasonal climates, especially those classified as Mediterranean (Parsons & Hopper 2003).

SOIL SEED BANKS

About 70% of SWAFR plants recruit from soil or canopy-stored seed as a primary or secondary means of recovery after fire (Appendix 1). These include about 6200 taxa with topsoil-stored seed, of which at least 5000 germinate most abundantly after fire. Inclusion of plants in this category does not imply germination is specifically promoted by heat and/or smoke, but these traits are especially common in the region (Roche *et al*. 1997; Cochrane *et al*. 2002; Merritt *et al*. 2007). Heat promotion of seed germination occurs in hard seeded Fabaceae, with over 1000 species in the Southwest and many species in this family globally (de Casas *et al*. 2017). Other plants that primarily regenerate from seed include 75% of studied Ericaceae species (Bell & Pate 1996) and many others in at least 59 families (Appendix 1).

In the SWAFR, soil seed banks include species with a wide diversity of dormancy mechanisms that commonly occur in combination (Roche *et al*. 1997; Cochrane *et al*. 2002; Merritt *et al*. 2007; Koch *et al*. 2009; Zirondi *et al*. 2019). This results in a continuum of seed types extending from those that are primarily optimised for short-term dormancy (to bypass adverse growing conditions), but germinate more abundantly after fire, to those where germination is primarily, or only, after fire. This evolutionary trend leads to long-term seed dormancy in many SWAFR species and culminates in obligate fire ephemerals. Some hard-seeded species can also germinate in response to extreme summer heat, a factor that could undermine soil seedbank sustainability in the future (Cochrane 2017).

Soil seed banks are important in both Mediterranean and arid environments in Western Australia and it would be expected that the seed remains viable for many years in both systems. However, the importance of seed germination promotion by fire is likely to be much greater in the Southwest where fire is much more frequent (Miller & Murphy 2017; Shedley *et al*. 2018). These traits are also important for restoration ecology, as the same species tend to emerge in severely disturbed topsoil (Rokich *et al*. 2000; Koch *et al*. 2009; Brundrett *et al*. 2020). For example, the majority of species present in a banksia woodland plant community (115 out of 160) recruited primarily from topsoil transferred to a new site (Fig. 11B), but this did not include trees or the majority of large shrubs that have canopy-stored seed (Brundrett *et al*. 2020). Many arid zone plants also have substantial fire adaptions such as topsoil- or canopy-stored seed (Commander *et al*. 2009; Erickson *et al*. 2018). Global data on species with persistent soil seed banks is limited. This trait is known from at least 15 plant families and 2566 species globally, but many of them have seeds that are viable for less than one year (Baskin *et al*. 2000; Gioria *et al*. 2019). In contrast, the majority of SWAFR plants have seeds that remain viable for decades in soil, particularly fire ephemerals that must survive long periods between fires.

CANOPY-STORED SEED

Storage of seeds for multiple years in the canopy is called serotiny, or bradyspory, but the former term is preferred (Lamont 1991). There are 1765 species with canopy-stored seed in five families in the SWAFR (Fig. 8, Appendix 1). This trait is most prevalent in the Myrtaceae (1143 taxa) and Proteaceae (448 taxa), but is also present in *Allocasuarina*, *Callitris* and samphires (Chenopodiaceae). About 420 serotinous species have seeds that are dispersed by wind after fire. Some Western Australia plants have extreme serotiny, such as the thick woody fruit that protects seed in hakeas and banksias. However, these structures also defend seed from granivorous birds, especially black cockatoos (Valentine *et al*. 2014; Groom & Lamont 2015). Only about 170 serotinous species are documented from outside Australia, including ~50 northern hemisphere conifers and 87 South African Proteaceae, but this is likely to be an underestimate (Lamont *et al*. 1991). At the other extreme it has been estimated that 8–20% of all plants globally have desiccation intolerant seed (Wyse & Dickie 2017), a trait that is rare in the SWAFR.

EXTREME FIRE SPECIALISTS

These plants are abundant by global standards in the SWAFR. These include fire ephemerals and orchid species that only flower after fire (Appendix 1). Some fire ephemerals also respond to soil disturbance so are not restricted to post-fire situations (Bell *et al*. 1984). Plants that are highly dependent on fire for growth or reproduction include:

1. At least 43 species of fire-ephemeral plants including annuals only found the first year after fire or perennials that persist for a few years after fire (Fig. 8, Appendix 1). These include most Gyrostemonaceae, *Brachyscias* (Fig. 9S) and some other Apiaceae, and members of 10 other families (Pate *et al*. 1985; Groom & Lamont 2015). Some of these annual species also have populations that germinate without fire (e.g. *Trachymene* spp.).
2. There also are at least 230 species with peak growth and reproduction after fire, followed by gradual attrition over several decades (Appendix 1). These include species of *Gompholobium*, *Bossiaea*, *Kennedia*

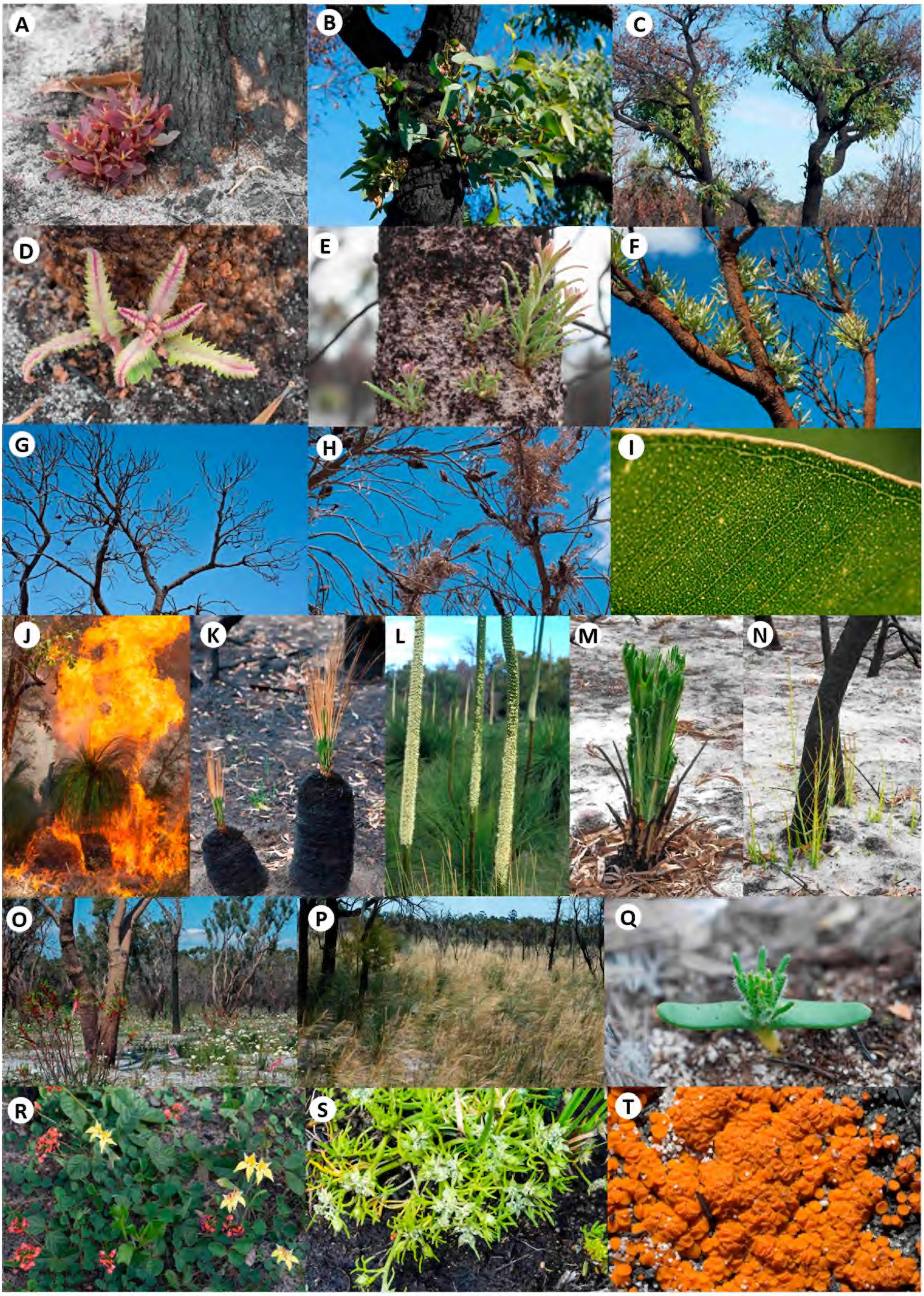

Figure 9. Illustrations of fire traits for selected southwestern Australian plants. Resprouting in *Eucalyptus todtiana* from A) the basal lignotuber, B) trunk, and C) crown; D) resprouting in *Banksia menziesii* from the lignotuber; resprouting in *B. attenuata* from E) the trunk or F) branches; G) *B. menziesii* killed at the time of thefire, or H) after resprouting; I) oil glands in leaf of *Eucalyptus tetraptera*; J) extremely flammable leaves of *Xanthorrhoea preissii*, but K) rapid regrow after fire, followed by L) abundant flowering; M) resprouting *Macrozamia riedlei*; N) *Nuytsia floribunda* resprouting from roots; O) temporary post-fire dominance by geophytes or P) the annual native grass *Austrostipa flavescens*; Q) germinating *Adenanthos cygnorum*; R) flowering promoted in *Caladenia flava* and *Kennedia coccinea*; S) the fire ephemeral *Brachyscias verecundus*; and T) the ash bed fungus *Anthracobia* sp.

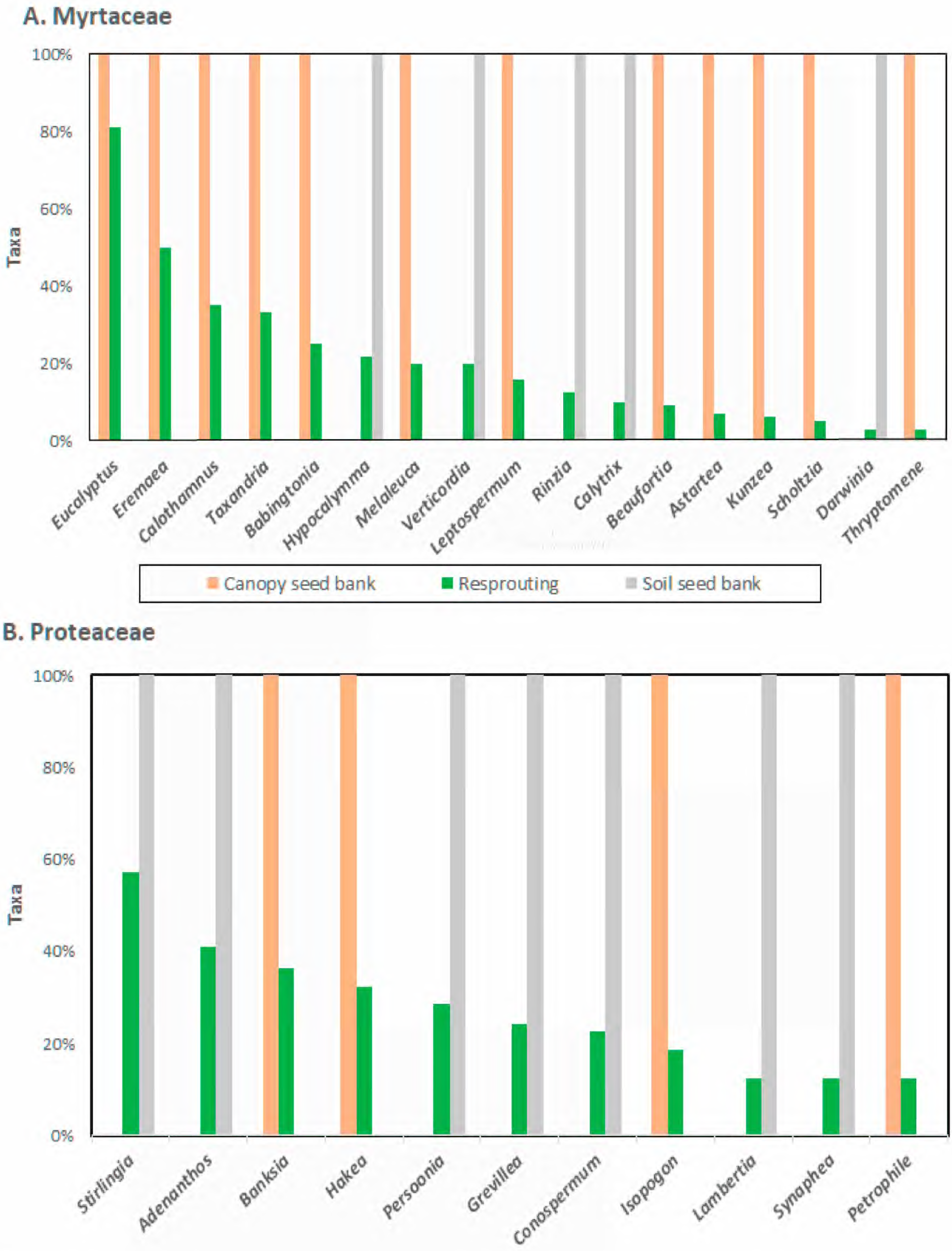

Figure 10. Case studies showing proportions of species with different fire trait specialisations in the largest genera within the plant families A) Myrtaceae and B) Proteaceae.

and *Viminaria* in the Fabaceae, as well as *Actinotus, Anthocercis, Macarthuria* and *Platysace*.

3 Fire promoted flowering occurs at least to some degree in over 3000 SWAFR species including many geophytes, resprouting and reseeding plants (Fig. 9R). This trait is also relatively common in the South African Mediterranean climate zone, but not elsewhere (Lamont & Downes 2011).

4 Pyrogenic flowering occurs in the Colchicaceae, Haemodoraceae, Orchidaceae and Droseraceae, etc. (Lamont *et al.* 2019). Their flowers are highly visible to pollinators, or have less competition for them, than many other plants that require years to begin flowering after fire (Burrows *et al.* 2008). Whereas many orchids flower prolifically after fire, some flower primarily (27 species) or only (10 species) after fire (Brundrett 2014). However, others are likely to be harmed by fire, as explained below.

FIRE AVOIDANCE

There are 1175 geophyte or annual taxa that can avoid fire through summer dormancy or as seed (Appendix 1). Others grow in habitats where fire is unlikely or impossible. These include aquatic and marine plants as well as arid zone plants or halophytes which have succulent foliage or grow in areas with sparse vegetation (Appendix 1). These may still have fire adapted traits but are not as well studied as plants in more fire prone areas. Annuals are expected to be able to avoid fire and/or recolonise sites due to wind-dispersed seeds, but some fail to reappear after severe fires (see **Winners and losers after fire**).

Fire trait complexity

1. There are 375 eucalypt taxa (*Eucalyptus* and *Corymbia*) in the region. These have variable fire traits, with 76% resprouting from lignotubers only, 1% resprouting from epicormic buds only and 6% resprouting from both (Fig. 9A–C). All species have canopy-stored seed so can germinate prolifically after fire (McCaw & Middleton 2015), but 18% lack resprouting capacity so only reseed (Appendix 1). Species with epicormic sprouting but no lignotubers may also primarily reseed after severe fires. Over 400 *Eucalyptus* species have lignotubers (Nicolle 2006; Clarke *et al.* 2015). Eucalypts also have highly flammable foliage (Bowman *et al.* 2014) due to oil storage in modified leaf cells called punctate glands (Fig. 9I). Their bark is either thick enough to protect trunks, or thin and frequently shedding, so contributes to the fuel load accumulating around tree bases (Grootemaat *et al.* 2017).
2. Fire-response complexity in myrtaceous shrubs such as *Melaleuca* includes canopy-stored seed in all species and about 25% of species that resprout from lignotubers (Fig. 10A, Appendix 1). In contrast, *Verticordia* is predominantly a reseeding genus of 94 species, but includes 14 resprouting species, including four with this trait in one subspecies but not in others (George & Pieroni 2002). Overall, there are >450 reported resprouters in 16 genera in the Myrtaceae (Fig. 10A), but the actual number would likely be over 700 when extrapolated to include data-deficient species. Many of these shrubs also have prominent oil storage glands in leaves or stems that increase their flammability.
3. There is similarly complex variability in resprouting capacity in Proteaceae taxa with canopy-stored seed or soil seed banks with fire-promoted germination, as well as >250 resprouters that also reseed (Appendix 1). There is a similar diversity of plants with canopy-stored (5 genera, 432 taxa), or topsoil-stored seed (9 genera, 487 taxa). These strategies are consistent within genera (Fig. 10B), but also help to define them. For example, *Hakea* is a monophyletic serotinous clade nested within *Grevillea* which are generally not serotinous (Mast *et al*. 2015). In contrast there are many separate origins of resprouting in the Proteaceae, which varies from none to all species in a genus (Fig. 10B). At least 11 *Banksia* or *Grevillea* species have resprouting ability that varies between subspecies. Variations in resprouting capacity and post-fire survival of banksias are linked to tree size and fire intensity (Figs 9D–H), but also vary over geographic ranges of species (Cowling & Lamont 1985).
4. Resprouting occurs in 10 Fabaceae genera, listed in decreasing sprouting frequency: *Hardenbergia, Hovea, Isotropis, Daviesia, Acacia, Bossiaea, Chorizema, Kennedia, Sphaerolobium Gastrolobium* and *Jacksonia*, but not in 31 others (Appendix 1). Resprouting occurs in 9 out of 60 species of *Acacia* examined (Burrows *et al*. 2008), but varies due to fire severity and bud depth (Wright & Clarke 2007). Overall, 6% of taxa in the Fabaceae resprout, with an extrapolated total of 18% of SWAFR species (Appendix 1).
5. Vigorous resprouting occurs from the stem and base of the arborescent monocots *Xanthorrhoea* spp., *Kingia australis* and *Dasypogon hookeri* (Lamont & Downes 1979; Staff & Waterhouse 1981). Growing points of these plants are protected by non-flammable leaf bases, but *Xanthorrhoea* leaves are extremely flammable overall (Figs 9J, K). These plants also flower most prolifically after fire (Fig. 9L).
6. Other examples of extreme fire recovery traits include anomalous wood in *Nuytsia floribunda* that allows resprouting from deep within its branches, but this tree also resprouts vigorously from roots (Fig. 9N). The cycad *Macrozamia riedlei* resprouts vigorously from its buried trunk (Fig. 9M). Resprouting from relatively fine roots also occurs in shrubs that 'sucker' such as species of *Lechenaultia* and *Isotropis*. These plants are virtually unkillable and flower most abundantly after fire. A similar strategy occurs in long-lived clonal plants including *Stirlingia latifolia* and *Hibbertia hypericoides*. The latter are two of the most dominant understory plants in banksia woodland, but may be non-clonal in other habitats.
7. Resprouting also occurs in over 1500 geophytes and at least 500 rhizomatous species (Appendix 1) that can flower prolifically after fire. Fire ephemeral grasses such as *Austrostipa* spp. that reseed also flower abundantly (Figs 9O, P).

FIRE INTOLERANCE

Plants that are killed by fire and lack a soil seed bank are less common than other categories (Fig. 8), but many plants become less dominant after fire. Mistletoes, which are killed when trees burn, can be dispersed by birds over moderate distances, but are lost from regions after large fires (Gosper & Prober 2020). Orchids such as *Pterostylis* and *Corybas* species are less likely to be seen after hot fires (166 taxa). These have relatively shallow tubers and prefer to grow in accumulated litter. The underground orchids (*Rhizanthella* spp.) should also be highly vulnerable to fire because they are fully reliant on mature plants of certain *Melaleuca* spp. for sustenance (Bougoure *et al*. 2010). The mycorrhizal fungi that orchids require to germinate and grow are most active in coarse soil organic matter (Brundrett *et al*. 2003), so frequent fires may indirectly impact on the abundance, diversity and vitality of all terrestrial orchids.

OTHER IMPORTANT TRAITS FOR SURVIVAL AND SPREAD

Many plants with canopy-stored seeds are dispersed by wind or animals after fire (Auld & Ooi 2017; Keith *et al*. 2020), including at least 1266 wind-dispersed plants (Appendix 1). Seed dispersal mechanisms involving birds, insects or other animals are also common for plants in the soil seed bank (Groom & Lamont 2015). Xerophytic plant traits occur in the majority of SWAFR perennial non-geophytic species and these traits are also common in other biomes. Reliance on intermediate or deep stored groundwater is important for trees and large shrubs that grow in summer (Zencich *et al*. 2002; Froend & Sommer 2010), including some banksias and many eucalypts. Many of these also flower in summer so have key roles supporting pollinators.

WINNERS AND LOSERS AFTER FIRE

SWAFR plants have a wide spectrum of inbuilt fire responses, but their survival is also regulated by fire intensity, frequency and seasonality (Godfree *et al*. 2021). Most habitats include fire ephemerals and fire intolerant species (Fig. 11A). Fire can also cause the loss of native annuals presumably because their seed was consumed with the litter (Bell *et al*. 1984; Brundrett & Longman 2016). Changes to vegetation structure last for years after fire and are primarily due to the altered dominance of plants, which is related to their fire traits (Hobbs & Atkins 1990; Burrows *et al*. 2008; Gosper *et al*. 2012; McCaw & Middleton 2015; Brundrett & Longman 2016; Etchells *et al*. 2020). Some reseeding native plants become much more dominant after fire in ecosystems and also tend to dominate young revegetation sites (Fig. 11B; Grant & Koch 1997; Brundrett *et al*. 2020). Disturbance opportunists such as species of *Gompholobium, Kunzea, Jacksonia, Acacia, Anthocercis, Kennedia* and *Adenanthos* (Fig. 9Q) can be abundant after fire but are relatively short lived. These include nodulated species of Fabaceae that help replace nitrogen, along with increased nodulation by *Allocasuarina* and *Macrozamia* (Hansen *et al*. 1987; Grove *et al*. 1980).

Fully aquatic and marine plants are fire avoiders, but plants in seasonal wetlands can be severely impacted. Peatlands are vulnerable to fire throughout Australia (Whinam & Hope 2005) and can be severely impacted

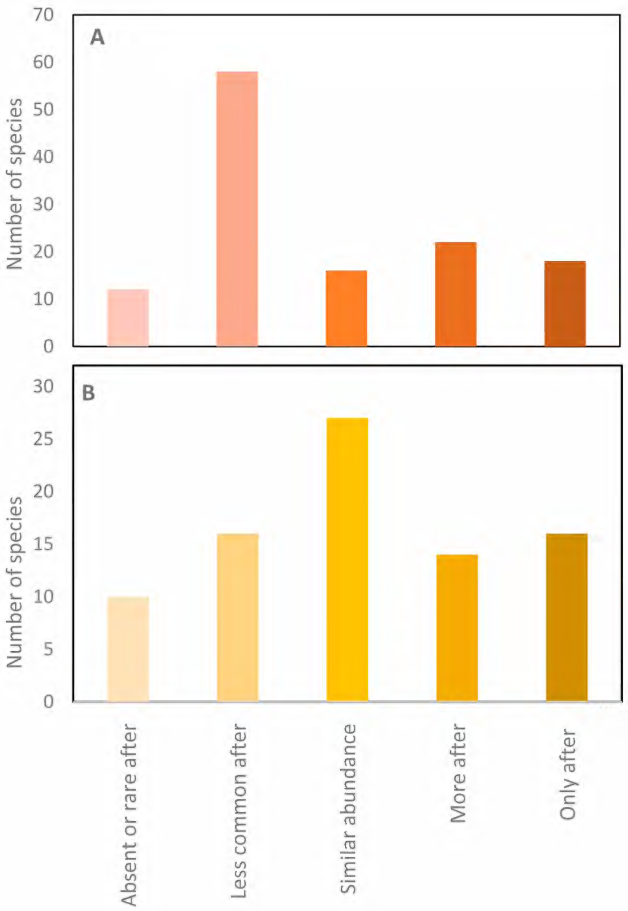

Figure 11. Responses of banksia woodland species to A) fire, or B) severe soil disturbance caused by topsoil transfer. Rankings are based on changes in the relative dominance of all plant species present (Brundrett *et al*. 2018, 2020).

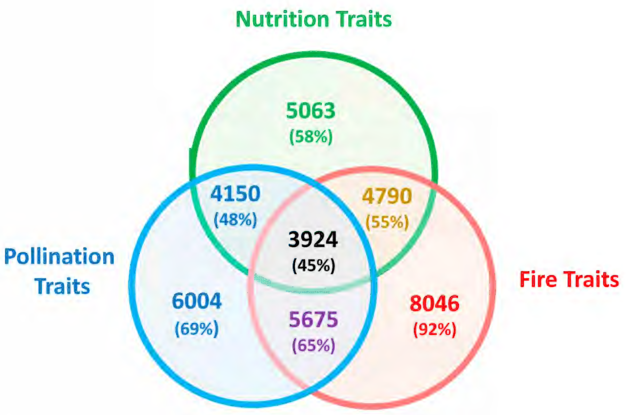

Figure 12. Venn diagram showing overlap in numbers of southwest Australian plants with relatively advanced nutrition, fire or pollination trait specialisations alone or in combination.

in the SWAFR (e.g. www.abc.net.au/news, accessed 19-2-2021). Ground fires can eliminate seed banks and resprouting structures when soil with high organic matter combusts (Bradshaw *et al*. 2018). Another commonly observed fire-response trend is for the dominance of weeds, especially grasses, exotic trees and annuals, to substantially increase at the expense of native plants (Hobbs & Atkins 1990; Milberg & Lamont 1995; Van Etten 1995; Fisher *et al*. 2009; Brundrett & Longman 2016). Common fire-promoted weeds include veldt grass (*Ehrharta calycina*), *Pelargonium capitatum*, pigface (*Carpobrotus edulis*) and weedy trees, especially exotic acacias and eucalypts. For example, one recent fire resulted in thousands of seedlings of *Acacia trigonophylla,* a non-local shrub uncommon before the fire (Keighery *et al*. 2017). Veldt grass alters the fuel composition potentially increasing the rate of spread of fires (Van Etten 1995).

Species that normally resprout strongly can be killed if severely burnt. For example, 51% of banksia trees died after an intense fire in Kings Park in 1989 (Bell *et al.* 1992) and 40% were killed by another in Banjup in 2014 (Brundrett & Longman 2016). Banksias can respond to fire by vigorously resprouting and reseeding (Fig. 9), but canopy structure requires years to recover (Brundrett *et al.* 2018), as is also the case in eucalypt forests (Wardell-Johnson *et al.* 2018a). Banksia seeds are also shed during drought providing some annual recruitment, but this increases dramatically after fire, resulting in thousands of seedlings per ha (McCaw & Middleton 2015; Brundrett *et al*. 2018). Most eucalypt species resprout and germinate from canopy-stored seed after fire, but 64 lack resprouting capacity so can only reseed (see text box, *Fire trait complexity*). Examples include *Eucalyptus salubris* (gimlet) and 43 relatively small trees (mallets). Species with epicormic buds but no lignotubers usually resprout, but may reseed only after extreme fires. These include *E. diversicolor* (karri), (Etchells *et al*. 2020), *E. salmonophloia* (salmon gum; Gosper *et al*. 2018) and *E. gomphocephala* (tuart). Overall, kwongan species with canopy-stored seed are less resilient than those with soil seed banks, or species which also resprout; however, even strong resprouters require some seedling recruitment to maintain populations (Enright *et al*. 2014). Impacts due to changes the fire severity or frequency, land clearing, as well as unsustainable timber harvesting, or grazing on SWAFR forests are of major concern due to their outstanding natural and cultural heritage values (Yates *et al.* 2017; Wardell-Johnson *et al.* 2018b). About half of the threatened flora species in the SWAFR are reseeders that are expected to be sensitive to increasing fire frequencies (Shedley *et al*. 2018).

Perennial plants have post-fire juvenile periods and most flower by year three, but trees can take more than seven to do so (Burrows *et al*. 2008; Brundrett *et al*. 2020; Wajon 2020). Soil seed banks may also be affected by long intervals between fires due to gradual declines in seed viability, as well as effective seed dispersal and seed predation. The longevity of seed in topsoil is largely unknown, but there are cases where plants may have persisted by this means for many decades and possibly centuries. Fire recovery requires at least 15–20 years in kwongan habitats, 25–30 years in sheoak or banksia woodland and up to a century to replace canopy seed stores in arid woodlands (Enright *et al*. 2011; Harvey *et al*. 2017; Valentine *et al*. 2014; Gosper *et al*. 2018). Resprouters also require time for storage reserves in lignotubers or rhizomes to build up, making them vulnerability to frequent fires (Enright *et al*. 2011). Furthermore, reduction in rainfall due to climate change is predicted to increase the minimum inter-fire interval required for self-replacement, placing many species at risk of decline (Enright *et al*. 2014).

Plants with multiple specialised traits

Trait complexity and transition frequency data (Fig. 13, Appendices 1, 2) suggest the following for plants in the SWAFR:

1. Relative to global averages, plants with advanced nutritional traits are substantially overrepresented (3–14 times greater than expected), many plants have highly specialised pollination syndromes with insects or birds (e.g. 2.5 times more than expected for birds) and an exceptionally high proportion of plants have complex acquired fire traits. For example, serotiny, soil seed banks and resprouting are orders of magnitude more common in the SWAFR than expected from global data.
2. Fire traits are highly variable and can differ between subspecies or even between populations of species, pointing to ongoing evolution in response to strong selective pressures (see text box, *Fire trait complexity*).
3. Pollination traits are also evolving relatively rapidly, as some vary within genera, especially due to switches to pollination by birds or specific insects.
4. Nutrition traits have switched the least frequently and are consistent in most families. However, variability is common in the three largest SWAFR families, where evolution is ongoing (see text box, *Nutritional trait complexity*).
5. Trait transitions are more complex for fire and pollination than nutrition, leading to more trait types and intermediate trait states.
6. Many SWAFR species have complex traits for nutrition, pollination and fire (Figs 3–10). Overlap between these trait categories shows that overall, 58% of taxa have at least one trait category, whereas 47–65% have advanced traits in two categories and 45% are advanced in all three (Fig. 12). Overall, plants with advanced traits for nutrition are also more likely to also have traits for fire and pollination, which appear to be increasing in complexity in parallel (Fig. 13, Appendix 2). Most SWAFR plants also have efficient traits for surviving severe drought, seed dispersal, resistance to grazing, etc., as is common in other biomes.
7. There are 14 plant families with a combined trait index of 10 or higher (Appendix 1). These include many endemic species in the SWAFR and their diversity patterns help define the regional boundary (Fig. 14).

Revising the SWAFR Boundary

Despite the well-recognised significance of the Southwest Australian Floristic Region (Diels 2007; Myers *et al*. 2000;

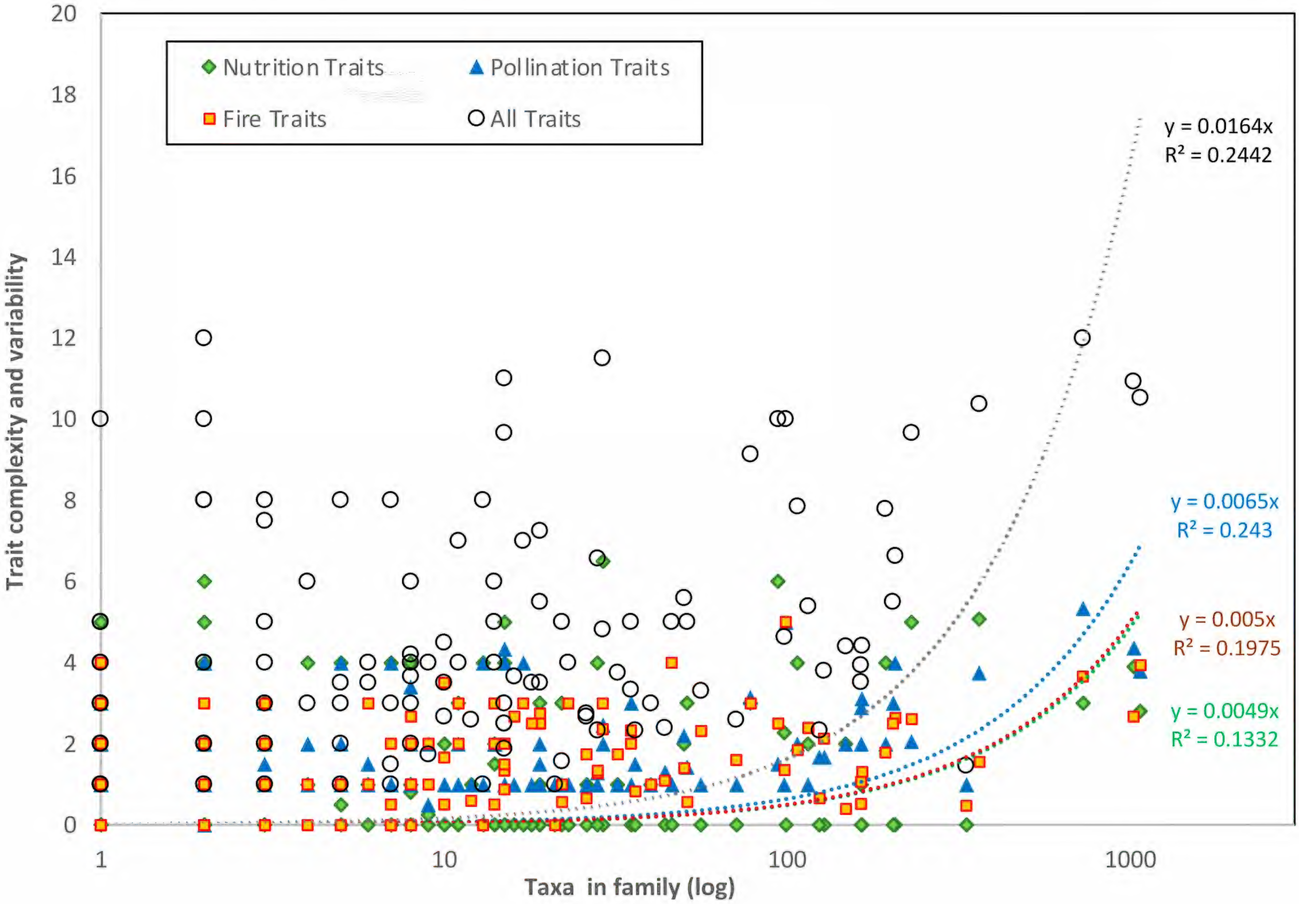

Figure 13. Comparison of the species richness of families of southwest Australian plants relative to complexity of their nutrition, fire and pollination traits, alone or in combination. Trait rankings are based on both the complexity and variability of traits for all taxa within families.

Hopper & Gioia 2004) defined regional boundaries for this region and methods used to define them differ considerably. Gioia & Hopper (2017) used plant species richness patterns and rainfall to define the SWAFR, but their plant diversity data did not extend far beyond their previously delineated boundary. Ebach *et al.* (2015) used the distributions and turnover for about 6000 plant species from nine widespread plant groups to demarcate a larger southwestern phytogeographical region. However, the extent of regions was not precisely determined in their analysis. Verboom & Pate (2015) used a combined analysis of soil and vegetation patterns to determine regional boundaries that were also similar to other studies. Long-term climatic fluctuations in the region (O'Donnell *et al.* 2018) and the recent contraction of the Mediterranean climate zone (Cross *et al.* 2020; grdc.com.au, accessed 3-3-2021) suggests that rainfall patterns cannot be used to define biogeographic regions. Vegetation patterns are strongly regulated by soils, landforms and hydrology (Fig. 1) and these remain much more stable over time.

The expanded SWAFR region boundary proposed here (Fig. 2) is more clearly demarcated than earlier proposed boundaries, as it corresponds with major discontinuities in the vegetation types mapped across Western Australia (Beard *et al.* 2013). Its boundary follows the inland margins of the Coolgardie and Yalgoo IBRA regions. The expanded bioregion includes three highly significant centres of plant diversity, rarity and endemism in the Coolgardie interzone: all of Forrestiana, the Mount Manning Region and the Great Western Woodlands (EPA 2007; Gibson *et al.* 2010; Harvey 2014; Hammer *et al.* 2018). For example, there are at least 1000 plant species including 9 rare, 72 priority and 32 endemic species in the Mount Manning Region (EPA 2007). The expanded bioregion also fully encompasses peak diversity hotspots for acacias (Hnatiuk & Maslin 1988; Bui *et al.* 2014) and eucalypts (Yates *et al.* 2017), the two most important genera in the region (Fig. 14). In addition, this results in a substantial increase of species endemism in the SWAFR (Fig. 14).

The addition of the two interzones into the SWAFR is justified because they contain vegetation that is more similar to the wheatbelt bioregion of the southwest botanical province than to the adjacent Eremaean or Nullarbor regions (Beard *et al.* 2013). Overall, there are six major vegetation types common to both the Coolgardie and wheatbelt regions, out of 13 overall. There is a gradual transition from the wheatbelt to the Coolgardie interzone, but the interzone–Eremaean transition encompasses abrupt changes from eucalypt- to acacia-dominated woodlands to the north and to chenopod-

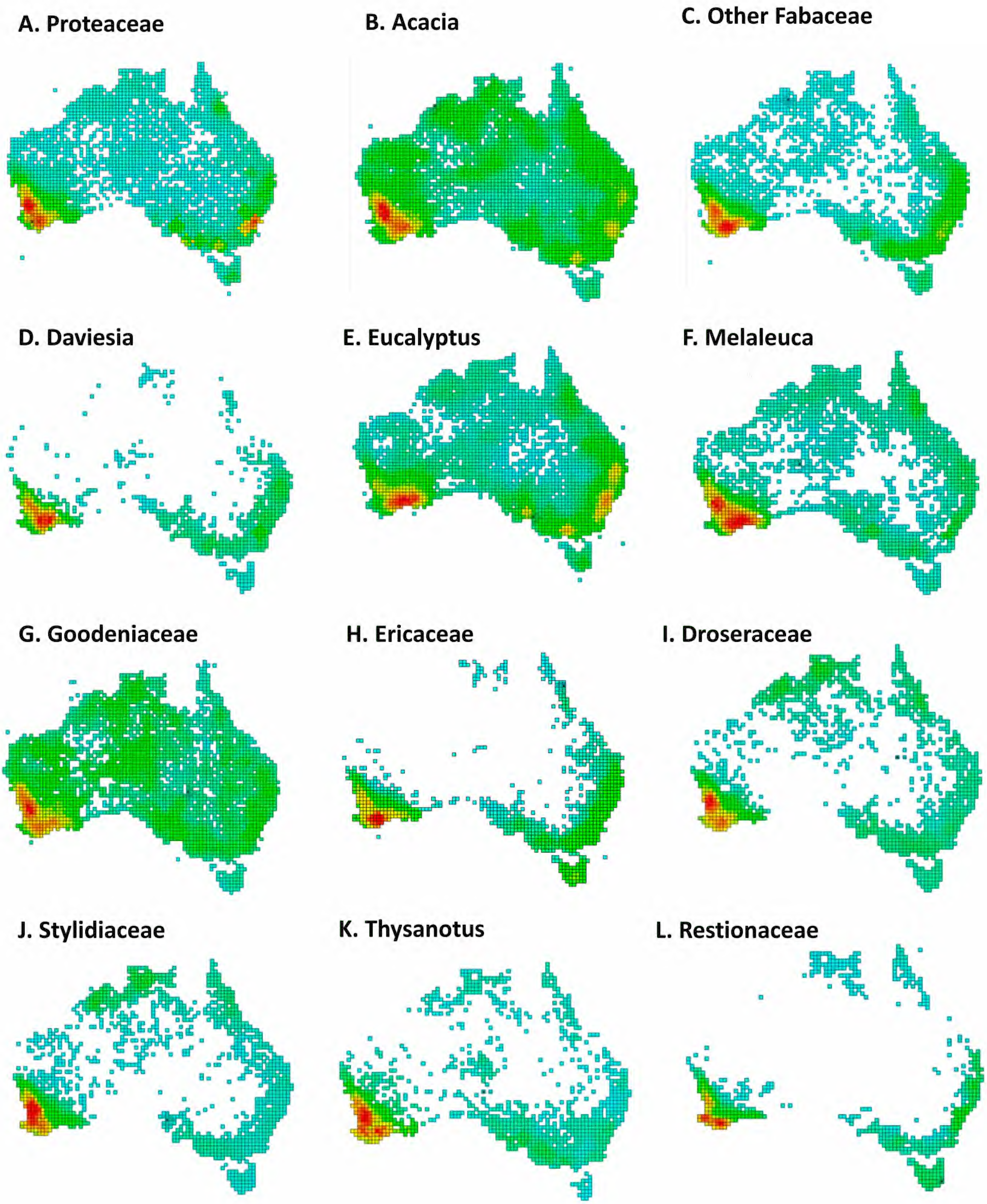
A. Proteaceae
B. Acacia
C. Other Fabaceae
D. Daviesia
E. Eucalyptus
F. Melaleuca
G. Goodeniaceae
H. Ericaceae
I. Droseraceae
J. Stylidiaceae
K. Thysanotus
L. Restionaceae

Figure 14. Spatial diversity patterns for selected clades of Australian plants with advanced traits for mineral nutrition, pollination and fire. Collections and observations data are plotted as a species richness index (ABC) using a moving window method, 1° cells and a 3° neighbouring area with Biodiverse software (Laffan *et al*. 2010).

dominated shrublands on alkaline soils across the Nullarbor to the east (Beard 2015). The narrow northern interzone (Yalgoo bioregion) has a mixture of vegetation types that are structurally more similar to wheatbelt than Eremaean vegetation (Beard *et al.* 2013). Both interzones include many poorly known species, especially where plant occurrence data is sparse (Gioia & Hopper 2017), but there is also limited data from the wheatbelt where extensive areas are largely cleared. Some habitat types typical of the SWAFR occur as localised patches in the Eremaean zone (Beard *et al*. 2013; Macintyre & Mucina 2021) and as far north as Cape Range next to Exmouth Gulf (Keighery & Gibson 1993). Specialised vegetation types like salt lakes and rock outcrops are important on both sides of the new SWAFR boundary but occupy relatively small areas.

An alternative designation for the biodiverse region in the Southwest is the Southwest Australian Trait Evolution Region (SWATER), given that it can be defined by the relative diversity of plants with extremely complex adaptations to local conditions (Fig. 14). This approach to defining regional boundaries utilises plant diversity to integrate all the complex interactions that regulate vegetation (Fig. 1) and plant trait complexity patterns to represent the evolutionary history of the region.

Trait evolution

Trait data was available for the majority of SWAFR plants (Appendix 1), but data availability varies between plant families and genera because some taxonomists are unconcerned about key functional attributes of plants whereas others use them to help define taxa. SWAFR plant diversity comparisons are also complicated by families or genera that include many unnamed species (Wege & Shepherd 2020), or apparent hybrids named as species (French & Nicole 2019). There are also many species complexes (closely related taxa that may intergrade) in the SWAFR where taxonomic variability can be overlooked (resulting in massive genetic divergence in ecotypes/provenances within species), assigned to subspecies, varieties or forma (e.g. Proteaceae), or divided into numerous similar species which cannot be readily identified (e.g. Orchidaceae). There are also major taxonomic issues, especially in the Proteaceae, Myrtaceae and Fabaceae, due to non-monophyletic genera (Orthia *et al.* 2005; Edwards *et al.* 2010).

Nutritional trait innovation complexity in the SWAFR includes many more clades than expected that include species with differing traits with overlapping functions (see text box, *Nutritional trait complexity*). clades represent a new wave of mycorrhizal evolution (Brundrett & Tedersoo 2018) which peaks in the SWAFR, as shown by the higher diversity of plants with advanced traits relative to other bioregions (Fig. 3). This strongly suggests that trait evolution is currently underway in the SWAFR and may even be accelerating (Brundrett 2017a; Brundrett & Tedersoo 2018). The highly infertile soil could explain why so many plants have switched from their ancestral AM symbiosis to EM or cluster roots, both of which are considered to be more energy intensive but also more effective at nutrient uptake when soil conditions are suitable (see text box, *Nutritional trait complexity*). Australia also is the source of a structurally unique mycorrhizal associations in the Asparagaceae (*Thysanotus* only) and the Rhamnaceae—a family that has EM associations here but not on other continents. Nitrogen fixation in the Fabaceae and Casuarinaceae may have caused a predisposition for acquisition of other nutritional traits (EM and cluster roots).

Key trends in pollination specialisation in the SWAFR involve the increased importance of birds and ground-dwelling animals, as well as specific interactions with insects, especially native bees, which are exceptionally diverse and specialised in the region (Keighery 1980; Brown *et al.* 1997; Houston 2018). These trends suggest that strong competition for general insect pollinators caused switching to more specific pollinators. However, pollinator declines and climatic impacts on pollination rates for plants in the region require further investigation (see text box, *Multidimensional interactions between fire, nutrition and pollination traits*).

The majority of Western Australian plant have one or more highly effective mechanism for fire recovery or avoidance that would not have been present in their distant ancestors. The most common strategy is for plants to rely on seed stored in topsoil for survival after being killed by fire. Fire responsive seeds have complex dormancy mechanisms that allow them to persist in soil for many years, followed by germination in response to cues such as heat or smoke. The second most common strategy is for plants to be partly consumed by fire but reuse part of their existing structure by resprouting. This strategy requires plants to store sufficient energy to support rapid regrowth and provides a considerable competitive advantage, especially for trees and large shrubs. The third common strategy is for plants to retain seed within protective structures for years, before their thick woody fruit or cones open for dispersal after fire (serotiny). Other common strategies include fire avoidance by summer dormancy in geophytes or as seeds for annual plants and post-fire flowering promotion (Appendix 1). Secondary traits that are also important in the SWAFR include efficient seed dispersal and long-term vegetative persistence, as well as tolerance to soil, climate or hydrology conditions (e.g. phreatophytic, xerophytic). There also can be an increased dominance of nitrogen fixing plants, which tend to produce more nodules after fire (Hansen *et al.* 1987; Grove *et al*. 1980).

In plant families with the most complex fire traits, such as the Proteaceae, Myrtaceae and Fabaceae, fire responses seem to be progressing from soil to canopy seed storage with fire-enhanced germination, to reseeding with some resprouting, then to primarily resprouting with some reseeding (Fig. 10). Resprouting capacity is gradually increasing in these families due to multiple origins of lignotubers and other subterranean storage organs. This trend is accompanied by increased importance of canopy seed protection, lignotubers and epicormic buds (Groom & Lamont 2015). Other fire traits that may occur in combination with these traits include thicker bark, wind dispersed seeds and fire-enhanced germination. Evolution in these families is complex and ongoing with some traits varying within species (see text box, *Fire trait complexity*). Resprouting also tends be more common in relatively large plants, which have invested more energy in persistent structures. This is best studied for *Banksia* species, which are more serotinous in semiarid shrublands on highly infertile soils (kwongan) than in woodlands on the Swan Coastal Plain (Cowling & Lamont 1985). In contrast, traits that originate infrequently, such as canopy or topsoil-stored seed are usually consistent within genera (Fig. 10).

Fire traits can also arise by modification of existing structures that initially increased survival in seasonally dry climates, such as resprouting from corms, bulbs or rhizomes. These plants presumably adapt to fire by increasing dormant bud protection by placement deeper in the soil or accumulation greater storage reserves. There also are examples of long-lived clonal forms of plants within otherwise non-clonal species (see text box, *Fire trait complexity*). Most rhizomatous species are monocots (Litsios *et al*. 2014; Howard *et al*. 2019), but some dicots have acquired modified woody roots with similar functions (Pate & Dixon 1982).

Variations in serotiny within families of SWAFR plants suggests that evolution of these traits must be ongoing (Lamont 2021). This incorporates multiple separate origins in the Proteaceae, which includes two species with a unique form of serotiny in *Conospermum* (Zhao & Ladd 2014). The evolution of persistent soil seed banks is more complex as this trait is also beneficial in areas where rainfall is highly seasonal or unreliable (de Casas *et al*. 2017). This includes hard seeded species, especially the Fabaceae, which can also be stimulated to germinate by mechanical scarification or fluctuations in heat without fire (Cochrane 2017). Extended seed dormancy can also result from increased apoplastic lipid barriers in seed coats (Renard *et al*. 2021). *Eremophila* fruit have a complex dormancy, which causes sporadic germination in arid regions but switches to fire-promoted germination in the Southwest (Richmond & Ghisalberti 1994; Chinnock 2007).

Seed germination that is enhanced by smoke has multiple origins in 58 separate SWAFR families and commonly occurs in combination with other seed dormancy mechanisms, so the role of seed ageing or priming is also important (Roche *et al*. 1997; Cochrane *et al*. 2002; Merritt *et al*. 2007; Koch *et al*. 2009; Zirondi *et al*. 2019). Fire-promoted seed germination can vary within species and smoke-responsive species can also germinate in response to severe soil disturbance, and perhaps could have been activated by digging native animals in the past. The final stage of this evolutionary trend leads to long-term persistence of seeds for fire-ephemeral plants, which are otherwise only present briefly after fire. One example of this is the annual herb *Brachyscias verecundus*, a rare annual Apiaceae species, which was considered to be almost extinct but reappeared in abundance after a recent fire (Fig. 9S).

The earliest angiosperms were likely to be disturbance opportunists that were much less competitive than the dominant gymnosperm trees (Wing & Boucher 1998) and were probably already responding to and benefiting from fire in the Cretaceous (Crisp *et al*. 2011; Carpenter *et al*. 2015). SWAFR plants have evolved to survive in a regime with infrequent hot fire and some have flammable leaves that can increase fire severity (Crisp *et al*. 2011). The high frequency of multiple fire traits in SWAFR plants suggests that one trait alone may not be sufficient to ensure the survival of species.

The changing nature of fire regimes in the 'Anthropocene' also need to be considered, as species that have survived infrequent hot fires for millennia may not be resilient to more frequent fires, even if they have relatively low intensity. As explained above, substantial intervals between fires are critical to the survival of many species, whereas others are only present briefly after fires (Fig. 11). Thus, maximising plants (and animal) diversity in ecosystems will require a mosaic that includes substantial areas of long-unburnt vegetation, as well as areas that have been burnt relatively recently. However, the optimal proportion of recently burnt areas may be much less than that of long-unburnt areas in many habitats due to the ability of plants that benefit from fires to persist for many decades in soil seed banks (see above). Most of what we know about fire ecology in Australia is based on unplanned hot fires in relatively undisturbed habitats. Much less is known about the long-term impacts of more frequent, relatively cool, fuel reduction burns early or late in the growing season, but these now traverse large areas each year (Bradshaw *et al*. 2018). Interactions between fire frequency and increased weed dominance also need to be considered.

As explained above, complex combinations of nutrition, pollination and fire traits are predominant in SWAFR plant species, especially in highly speciose and taxonomically complex clades (Appendix 2) Some of these clades are known to have relatively fast rates of evolution and/or low rates of extinction relative to other Australian plants and diversified rapidly in parallel with the aridification of Australia in the past 25–30 Ma (Crisp & Cook 2013; Toon *et al*. 2014; Cook *et al*. 2015; Groom & Lamont 2015; Cardillo *et al*. 2017; Mast *et al*. 2015). However, interactions between net diversification and extinction rates vary considerably between taxa and regions, and over time (Cook *et al*. 2015; Cardillo *et al*. 2017; Nge *et al*. 2020a). Plants that migrated into arid regions such as the Amaranthaceae have also become successful in the SWAFR (Hammer *et al*. 2019).

Australian temperate plants (and their associated fungi) are being dispersed globally by humans and can become major weeds elsewhere. These include highly invasive members of the Myrtaceae (*Eucalyptus* and *Melaleuca*), as well as *Acacia* and *Casuarina* species (Richardson & Rejmánek 2011). In addition to leaving most pests and diseases behind, SWAFR plants with several of the following traits are likely to be highly successful invaders in exotic locations:

1 Rapid growth, efficient dispersal and drought tolerance.

2 Rapid recovery and/or enhanced dispersal after fire due to multiple fire traits.

3 Nutritional trait flexibility such as dual mycorrhizal associations or the capacity to form cluster roots.

4 Nitrogen fixation (Casuarinaceae and Fabaceae).

5 General insect or wind pollination.

Factors that lead to highly successful invasions of exotic plants in Australia also include many of these traits. For example, many weeds have wind or general insect pollination and benefit from fire in the SWAFR.

Trait data in Figure 13 shows that the most successful and diverse SWAFR plant clades also tend to be the most specialised. Cowling *et al*. (1994) determined Mediterranean climate diversity hotspots contained many edaphic specialists, especially members of the Fabaceae, Proteaceae, Cyperaceae, Ericaceae, Myrtaceae, Restionaceae and Asteraceae. Selection pressures that drive trait evolution are similar in many regions, but plants have had less time for extreme specialisation to appear in most of them. For example, tropical ecosystems include many species with highly specialised pollination and seed dispersal syndromes (Willmer 2011; Wenny *et al*. 2016) but tend to have fewer specialised traits for nutrition or fire. Fire is also important in savannah and prairie grasslands (Maurin *et al*. 2014), but there is less evidence of extreme nutrition and pollination specialisation. The South African Floristic Region may well be the second-most trait complex flora globally, due to many species with complex fire and pollination traits (Cowling *et al*. 1994; Johnson & Steiner 2003), but it has fewer clades with nutrient trait switching than the SWAFR (Brundrett 2017a). Thus, the extreme nature of selective pressures for multiple trait categories seems to be unique to the SWAFR, which may have the most specialised flora on earth.

Multidimensional interactions between fire, nutrition and pollination traits

A. Fire–Nutrition

i. Fire responses and nutrient strategies are linked, with EM, cluster root and nitrogen fixing species more dominant in fire-prone habitats (Pekin *et al*. 2012).

ii. Fire causes major losses of volatile nutrients such as nitrogen, and other nutrients are redistributed or lost to wind and water erosion of damaged soils (Grove *et al*. 1986).

iii. Increased nutrient availability (except for nitrogen) at the soil surface promotes rapid growth of reseeders (Grove *et al*. 1986).

iv. Nitrogen deficits post-fire are redressed by abundant nitrogen fixing plants such as acacias and peas, cycads and *Allocasuarina* spp. (Hansen *et al*. 1987; Grove *et al*. 1980).

v. Fire ephemeral fungi such as *Anthracobia* sp. (Fig. 9T) and bryophytes seem to have major roles in initial soil and nutrient stabilisation (McMullan-Fisher *et al*. 2011).

vi. Some reseeders and resprouters take advantage of increased soil fertility post-fire, but become less common in long inter-fire periods (Grove *et al*. 1986; Brundrett *et al*. 2018).

vii. Mycorrhizal associations are likely to be suspended after fire as defoliated trees can lack the energy to support mutualists. Mycorrhizal fungus diversity substantially declines when trees are severely damaged (Robinson & Bougher 2003; Anderson *et al*. 2010).

viii. The nutrient cycling system for litter and wood could take years to recover after fire due to impacts on saprophytic fungi, invertebrates and digging mammals.

B. Fire–Pollination

i. Flowering abundance increases briefly after fire for some insect pollinated plants.

ii. Resources for nectivorous birds could be scarce for several years due to the slow recovery of large shrubs and trees.

i. Many native bees that nest in holes in dead wood (Houston 2018) would perish, potentially leading to pollination shortages, especially for sort-lived reseeders after fire.

iii. Long-term reductions in pollination efficiency due to insect decline (Sánchez-Bayo & Wyckhuys 2019) could have a major impact on seed bank restocking after fire. This would reduce the competitive advantage of reseeders and extend safe inter-fire intervals.

iv. Non-flying mammal pollinators are likely to be rare or missing after fire (Bradshaw 2014).

v. Some wind pollinated plants grow primarily after fire (e.g. Gyrostemonaceae).

C. Pollination and other animal roles–Nutrition

i. Excess energy in plants with slow growth in highly infertile soils can lead to increased switching from insect to bird or animal pollination (Orians & Milewski 2007).

ii. Seed accumulation in canopy and soil seed banks would lead to declining overall available nutrient stocks with time since fire in fire prone ecosystems.

iii. Seed eating birds such as black cockatoos are likely have an important role to redistributing nutrients tied up in seeds in these ecosystems.

iv. Impacts on soil digging animals such as bandicoots on nutrient cycling can be severely interrupted by fire (Fleming *et al*. 2014).

v. Animal species that formerly dispersed hypogeal mycorrhizal fungi are now absent in most parts of the SWAFR.

D. Interactions altered by severe climatic conditions

i. Seedlings can perish post-fire due to severe drought.

ii. Severe drought also reduces the capacity for plants to resprout or restock seed banks.

iii. Severe drought can reduce flowering and seed production (e.g. Brundrett 2019).

iv. Recently burnt ecosystems may have greater supplies of water in the short term due to greatly reduced transpiration (Mappin *et al*. 2003).

SWAFR plants have evolved a three-way combination of acquired traits for (1) nutrition, (2) fire and (3) pollination (Fig. 12). It seems that these three opposing drivers of evolution are generally not in conflict, or do not greatly reduce competitive ability, due to their combined costs. Evolution of these traits would be driven by highly infertile soils, fires, as well as drier and more variable climates, all of which have all increased in severity and in parallel since the Cretaceous (Lamont *et al*. 2011; Gosper *et al*. 2019). For example, Orians & Milewski (2007) noted that both bird pollination, which requires abundant nectar in flowers, and increased flammability of plants likely result from slow plant growth in extremely infertile soils leading to surplus energy stored in Australian plants. Pausas & Lamont (2018) also noted the 3-dimensional nature of trait evolution, but they assigned broader trait categories to major axes (environment, disturbance and biotic interactions). Thus, there are more than three important interacting axes that drive plant evolution overall. However, triangular (or 3D) conceptual models are especially useful for illustrating the complexity of trait-species interactions. The text box '*Multidimensional interactions between fire, nutrition and pollination traits'* provides examples of these interactions that impact on the management of ecosystems and threatened species.

The unique nature of SWAFR plant trait specialisations leads to a number of key unanswered questions:

1. Why are some traits consistent within families (or orders) whereas others vary within species?
2. Why are plants with complex traits so prevalent in this region?
3. Why do new traits arise more often within clades that already have complex acquired traits?
4. Can traits be classified as fundamental (required to avoid extinction), or adaptive (acquired to increase competitive ability)?
5. Is extreme trait specialisation risky for plants and thus linked to the abundance of rare plants?

CONCLUSIONS

Diversity maps show that the majority of Australian plants in trait-complex clades, which are also highly speciose and taxonomically complex, have distributions centred in the SWAFR. These plants tend to be exceptionally well adapted to infertile soils, have relatively advanced pollination strategies and also have one or more acquired fire recovery traits. These traits evolved over long periods due to intense competition for soil nutrients and pollinators and the need to survive fires. Similar evolutionary trends also apply to a lesser degree in the rest of Australia and other regions with a Mediterranean climate.

There is now evidence that the complex trait strategies of SWAFR plants are becoming less effective due to reduced beneficial fungal activity, pollinator decline and substantial increases in fire severity and frequency. Threats to biodiversity both locally and globally include accelerating habitat loss and degradation due to fire, weeds, drought and pollinator decline (Sánchez-Bayo & Wyckhuys 2019; Bell & Callow 2020; Godfree *et al*. 2021; Bergstrom *et al*. 2021). The SWAFR is now considered to be prone to ecosystem collapse due to climate change interacting with these factors (Bergstrom *et al*. 2021; Ritchie *et al*. 2021).

This paper amalgamates information from several disparate disciplines that study plant adaptations to environmental stresses in Australia. Experts in these disciplines (e.g. ecologists, entomologists, mycologists, restoration ecologists and seed biologists) all know of extreme cases of specialised plant traits and exceptionally complex interactions with fungi or animals, but this knowledge has to be combined to reveal how unique the SWAFR is. This broad-based knowledge is essential to conserve threatened species, restore habitats and sustainably manage ecological communities (see text box, *Multidimensional interactions between fire, nutrition and pollination traits*). However, caution is required when scaling trait data from individual plants up to ecosystems and avoid using simplified concepts in ecosystem management.

Globally, the southwest Australian biodiversity hotspot arguably has the most highly complex combination of plant traits that promote survival in fire-prone and infertile habitats, and efficient pollination. This assertion is supported by correlations between the taxonomic diversity of plant clades in the region and their trait complexity. The SWAFR should also be designated as an advanced trait evolution region (SWATER), because its boundaries can be defined by the relative diversity of the plants with highly complex functional traits, along with vegetation and soil patterns. This approach for defining bioregions integrates key trends in evolutionary history with interacting factors that currently regulate distributions of vegetation types and species. Due to the extreme complexity of interactions between plant functional traits and environmental stresses in the region, the SWAFR is the best location on earth for studying the long-term impacts of these factors on plant evolution, physiology, genomics and diversity. This bioregion also provides a preview of conditions elsewhere on earth in the future, when many plants will need to survive in more flammable habitats with fewer pollinators and less fertile soils.

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Appendix 1. Summary of acquired traits for nutrition, fire or pollination in plants from southwestern Western Australia. Trait categories, complexity and variability are summarised for families or genera when they vary within families (with number of taxa). See Table 1 for abbreviations (CV = complexity and variability index).

Family	Genera	Species	Taxa	Plant Nutrition Traits			Pollination Traits		Fire Response Traits				CV
				Nutrition	Habitat	CV	Syndrome	CV	Seed	Sprouting	Ecology	CV	sum
Ferns													
Aspleniaceae	2	5	6	AM		0	WDS	0	WDS	RLR		1	3.5
Dennstaedtiaceae	1	1	1	AM, LRH		1	WDS	0	WDS	RLR	FPF	2	5
Isoetaceae	1	8	9	AM, LRH		0	WDS	0	WDS	RCB (9)	NSH	1	4
Lindsaeaceae	1	1	1	AM, LRH		0	WDS	0	WDS	RLR		1	4
Lycopodiaceae	1	1	1	AM, LRH		2	GIP	2	WDS	RCB (1)		1	5
Marsileaceae	2	6	6	AM (NM), LRH		2	Water	3	WDS	RCB (5)	NSH	1	3.5
Ophioglossaceae	1	3	3	AM		2	GIP	0	WDS	RCB (3)	NSH	1	5
Psilotaceae	1	1	1	AM		2	WDS	2	WDS		SIm	1	5
Pteridaceae	4	9	10	AM, LRH		1	WDS	2	WDS	RLR	FPF	1	1.8
Salviniaceae	1	2	2	NM, no roots	Aqua	4	Water	0	WDS		NSH	0	8
Schizaeaceae	1	2	2	AM, LRH		0	WDS	0	WDS	RLR	SIm	1	4
Selaginellaceae	1	1	1	AM (NM)		0	WDS	0	WDS		SIm	0	3
Thelypteridaceae	1	1	1	AM, LRH		1	WDS	2	WDS	RLR		1	4
Gymnosperms													
Cupressaceae	1	9	9	AM		0	Wind	2	CSB	RLR (1)	SIm	2	4
Podocarpaceae	1	1	1	AM		0	GIP	3		RLR	FPF	2	5
Zamiaceae	1	3	3	AM, N2F		2	SIP	3		RLR	FPF	3	8
Monocots													
Acanthaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Aizoaceae	6	26	27	NM	ASD	1	GIP	1	SSB, GPF (4)	RCB (1)	FPF (4), NSH	0.7	2.7
Alismataceae	1	1	1	NM (AM)	Aqua	3	GIP	1			NSH	0	4
Amaranthaceae	5	50	59	NM, LRH	ASD	2	GIP, SIP	2.2	SSB, GPF?	RCB (3)	FPF (4), FAA (6), NSH (53)	1.4	5.6
Anarthriaceae	3	11	11	NM, SBR		3	Wind	2	SSB, GPF	RLR	FPF	2	7
Aphanopetalaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Apiaceae	13	56	61	AM		0	GIP	1	SSB, GPF	RLR (19)	FPF (59), FE (3), SAF (19)	2.3	3.3
Apocynaceae	4	7	7	AM		0	GIP	1	SSB, GPF	RLR (1)	SIm (5)	0.5	1.5
Apodanthaceae	1	2	2	NM, Para	Internal	6	SIP	4			SIm (2)	0	10
Aponogetonaceae	1	1	1	NM	Aqua	1	GIP	1			NSH	0	2
Araceae	2	2	2	NM	Aqua	4	Water	4			NSH	0	8
Araliaceae	3	35	37	AM		0	GIP	1	SSB, GPF (13)	RLR (1)	FPF (36), FE (4), FAA (13)	2.3	3.3
Asparagaceae	10	115	123	AM, or Thys (52)		2	GIP	1	SSB, GPF (102)	RLR (41), RCB (47)	FPF (104), SAF (15), SIm (18)	2.4	5.4
Asphodelaceae	1	1	1	AM		0	GIP	1	SSB, GPF	RCB (1)	FPF, FE	2	3
Asteraceae	92	332	368	AM		0	GIP	1	SSB, GPF (152)	RLR (8)	FPF (155), FE (5), FAA (260)	0.5	1.5
Boraginaceae	7	22	28	AM		0	GIP	1	SSB, GPF?		FPF (24), FAA (3), NSH (3)	0.6	1.6
Boryaceae	1	7	7	AM		0	GIP	1	SSB, GPF?	RLR	NSH	2	3
Brassicaceae	11	40	41	NM, LRH	ASD	1	GIP	1	SSB, GPF (1)		FPF, FAA	1	3
Burmanniaceae	1	1	1	AM (NM)	Aqua	2	GIP	1	SSB		NSH	0	2
Byblidaceae	1	2	2	NM, Carn		5	SIP	4	SSB, GPF		FPF, FE	3	12
Campanulaceae	3	23	25	AM		0	GIP	1	SSB, GPF (21)	RLR (1)	FPF (25), FAA (11)	3	4
Capparaceae	1	1	1	NM, LRH	ASD	2	GIP	1			NSH	0	3
Caryophyllaceae	3	8	8	NM, LRH	ASD	1	GIP	1	SSB, GPF?		FPF (2), FAA	1	3

Casuarinaceae	2	29	33	EM-AM, CR AM, N2F,		6.5	Wind	2	CSB, WDS	RLR (450), RAG (7)	NSH (2)	3	11.5
Celastraceae	3	16	19	AM		0	GIP	1	SSB, GPF (15)	RLR (3)	FPF (19)	2.7	3.7
Centrolepidaceae	2	19	23	NM, LRH	Aqua	1	Wind	2	SSB, GPF?		FPF (18), FAA (23)	2.5	5.5
Cephalotaceae	1	1	1	NM, Carn		5	GIP	1	SSB, GPF	RLR (1)	FPF, FE	4	10
Chenopodiaceae	20	148	180	NM, LRH	ASD	2	Wind	2	SSB (80), CSB (134), WDS (38)		NSH (150)	0.4	4.4
Colchicaceae	2	19	26	AM		0	GIP	1	SSB, GPF (5)	RCB (26)	FPF (5)	2.5	3.5
Commelinaceae	1	1	1	NM, LRH	ASD	1	GIP	1	SSB, GPF	RCB	FPF, SAF	3	5
Convolvulaceae	8	15	16	AM		0	GIP	1	SSB, GPF?	RLR (9)	FPF (8), NSH	0.9	1.9
Crassulaceae	1	8	11	NM	ASD	1	GIP	1	SSB, GPF		FPF, FAA	2	4
Cymodoceaceae	4	5	5	NM	Marine	4	Water	4			NSH	0	8
Cyperaceae	24	193	268	NM (AM), DR		4	Wind	2	SSB, GPF (178)	RLR (195), RCB (2)	FPF (37), FAA (18), SIm (4)	1.8	7.8
Dasypogonaceae	4	19	19	NM, SBR		3	SIP, GIP	1.5	SSB, GPF	RLR (450), RAG (1)	FPF (19), SIm (1)	2.8	7.3
Dicots													
Dilleniaceae	1	99	114	AM		0	SIP, BP	5	SSB, GPF	RLR (17)	FPF (114), SAF (2)	3	10
Dioscoreaceae	1	1	1	AM		0	GIP	1	WDS	RLR	FPF	2	3
Droseraceae	2	94	109	NM, Carn, LRH		6	GIP	1.5	SSB, GPF	RCB (58)	FPF (108), NSH (1)	2.5	10
Ecdeiocoleaceae	2	3	3	NM, SBR		3	GIP	1.5	SSB, GPF	RLR	FPF	3	7.5
Elaeocarpaceae	3	35	39	AM		0	SIP	3	SSB, GPF	RLR (1)	FPF (39), NSH (6)	2	5
Elatinaceae	2	5	5	AM		0	GIP	1			SIm (5)	0	1
Emblingiaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Eremosynaceae	1	1	1	AM		0	GIP	1	SSB, GPF		FPF, SAF	2	3
Ericaceae	18	230	343	Eric		5	SIP, Bird, NFM	2	SSB, GPF	RLR (39)	FPF (19), SAF (11)	2.6	9.7
Euphorbiaceae	10	71	79	AM		0	GIP	1	SSB, GPF	RLR (3)	FPF (23), SAF (6), NSH (11)	1.6	2.6
Fabaceae	42	1021	1204	AM, EM-AM, NM, CR, N2F		3.9	GIP, SIP, Bird, BPB	3.1	SSB, GPF	RLR (86)	FPF (330), SAF (31), FAA (2), NSH (50)	2.7	10.9
Frankeniaceae	1	21	24	AM	ASD	0	GIP	1	SSB, GPF?		NSH	0	1
Gentianaceae	2	3	3	AM		0	GIP	1	SSB, GPF?		NSH	0	1
Geraniaceae	3	8	8	AM		0	GIP	1	SSB, GPF, WDS (4)	RLR (3)	FPF, FAA (2)	2.7	3.7
Goodeniaceae	11	206	236	AM		0	SIP	4	SSB, GPF (146)	RLR (35)	FPF (155), SAF (13)	2.6	6.6
Gyrostemonaceae	5	14	17	AM		0	Wind	2	SSB, GPF		FPF, FE	3	5
Haemodoraceae	7	78	109	NM, SBR		3	Bird, GIP, SIP	3.1	SSB, GPF (96)	RLR (27), RCB (16)	FPF (109), FE (5), SAF FAA (2)	3	9.1
Haloragaceae	7	51	60	AM, NM (AM)	Aqua (14)	3	GIP	1.4	SSB, GPF (18)	RLR (4)	FPF (22), SAF FAA (1), NSH (33)	0.6	5
Hemerocallidaceae	11	29	47	AM		0	GIP	2.4	SSB, GPF (34)	RLR (30), RCB 8)	FPF (34), SAF (3), SIm (2)	2.4	4.8
Hydatellaceae	1	5	5	NM	Aqua	1	GIP	1	SSB		FPF, FAA, NSH	1	3
Hydrocharitaceae	5	8	8	NM	Marine	4	Water, GIP	3.4			NSH	0	4.2
Hypericaceae	1	2	2	AM		0	GIP	1	SSB, GPF?		FAA	1	2
Hypoxidaceae	1	5	8	AM		0	GIP	1	SSB, GPF?	RCB (8)	FPF	1	2
Iridaceae	2	18	25	AM		0	GIP	1	SSB, GPF	RLR (23), RCB (2)	FPF (20)	2.5	3.5
Juncaceae	2	14	15	NM, LRH		2	Wind	2	SSB, GPF?	RLR (10)	FPF FAA (1)	2	6
Juncaginaceae	2	14	16	NM	Aqua	1	Wind	2	SSB		FAA (4), NSH (2)	0.5	4
Lamiaceae	19	165	193	AM		0	SIP, GIP	3.1	SSB, GPF (52)	RLR (4)	FPF (21)	1.3	4.4
Lauraceae	1	8	13	NM, Para		4	GIP	1	SSB, GPF		SIm (13)	1	6
Lentibulariaceae	1	15	15	NM, Carn	Aqua	5	SIP	4	SSB, GPF?	RLR (1)	FPF, FAA	2	11
Linaceae	1	1	1	AM		0	GIP	1	SSB, GPF?		FAA (1)	1	2
Loganiaceae	4	26	27	AM		0	GIP	1	SSB, GPF (14)	RLR (3)	FPF (8), FAA (5)	1.8	2.8
Loranthaceae	3	15	18	NM, Para	Mistletoe (17)	4	Bird, GIP	4.3			FPF (1), SIm (17)	1.3	9.7

Appendix 1. (cont.).

Family	Genera	Species	Taxa	Plant Nutrition Traits			Pollination Traits		Fire Response Traits				CV sum
				Nutrition	**Habitat**	**CV**	**Syndrome**	**CV**	**Seed**	**Sprouting**	**Ecology**	**CV**	
Lythraceae	1	1	1	AM		0	GIP	1	SSB		FAA (1)	1	2
Malvaceae	18	164	191	AM		0	SIP, GIP	2.9	SSB, GPF (109)	RLR (5)	FPF (103), SAF (11), NSH (19)	1.1	3.9
Meliaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Menyanthaceae	2	10	10	NM	Aqua	2	GIP	1	SSB	RLR (2)	NSH	0.5	3.5
Molluginaceae	3	8	8	AM		0	GIP	1	SSB, GPF (5)	RLR (1)	FPF SAF (5), NSH (3)	1	2
Myrtaceae	48	1066	1510	AM, EM-AM, EM (AM)		2.8	GIP, SIP, Bird, NFM, SPP	2.4	SSB GPF (367), CSB (1143), WDS (210)	RLR (450), RAG (42)	FPF (218), SAF (64), SIm (27), VFF (834)	3.9	10.5
Nitrariaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Nyctaginaceae	2	3	3	AM		0	GIP	1			SIm (3)	0	1
Olacaceae	1	4	4	AM		4	GIP	1	SSB, GPF?		FPF SAF (1)	1	6
Oleaceae	1	2	3	AM		0	GIP	1	SSB			0	1
Onagraceae	1	2	4	AM		0	GIP	1	SSB, WDS, GPF?		FPF, FAA	1	2
Orchidaceae	27	362	428	Orchid		5.1	SIP, GIP, SD, VD	3.7	WDS (426)	RLR (1), RCB 427)	FPF (263), SIm (78),	1.6	10.4
Orobanchaceae	2	1	2	AM		0	GIP	1	SSB, GPF?		FAA	1	2
Oxalidaceae	1	3	3	AM		0	GIP	1		RCB (3)	FAA (3)	2	3
Pedaliaceae	1	1	1	AM		0	GIP	1	SSB, GPF		SIm (1)	0	1
Philydraceae	1	2	4	AM		1	GIP	1	SSB, GPF?	RCB (4)	FPF, FAA	2	4
Phrymaceae	4	7	7	AM		0	GIP	1	SSB, GPF?		FAA (1)	0	1
Phyllanthaceae	3	15	15	AM		0	GIP	1	SSB, GPF (14)	RLR (3)	FPF, SAF (4)	2	3
Pittosporaceae	6	36	36	AM		0	GIP	1.5	SSB, GPF (17)	RLR (19)	SIm (2), NSH (3)	0.8	2.3
Plantaginaceae	4	13	13	AM		0	GIP	1	SSB		FAA (6)	0	1
Plumbaginaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Poaceae	53	164	182	AM, LRH		1	Wind	2	SSB, GPF (68)	RLR (15)	FPF (94), FAA (11), NSH (90)	0.5	3.5
Polygalaceae	1	17	17	AM		0	GIP	4	SSB, GPF	RLR (17)	FPF	3	7
Polygonaceae	5	12	12	NM, LRH	ASD	1	GIP	1	SSB, GPF (3)		FPF (3), FE (1), FAA (4), NSH (5)	0.6	2.6
Portulacaceae	4	32	36	NM	ASD	1	GIP	1	SSB, GPF (34)	RCB (8)	FPF (34), FE (1), FAA (1)	1.8	3.8
Posidoniaceae	1	7	7	NM	Marine	4	Water	4			NSH	0	8
Potamogetonaceae	4	13	14	NM	Aqua	4	Water, Wind	5			NSH	0	8
Primulaceae	1	3	6	AM		0	GIP	1	SSB, GPF?		FPF	1	2
Proteaceae	15	726	928	NM, CR		3	SIP, Bird, GIP, NFM, SPP	5.3	SSB GPF (565), CSB WDS (446)	RLR (450), RAG (10)	FPF (161)	3.7	12

Ranunculaceae	3	10	13	AM		0	GIP	1	SSB, GPF (9)	RLR (4)	FPF (4), FE FAA (1)	1.7	2.7
Restionaceae	20	107	111	NM (AM) DR, SBR		4	Wind	2	SSB, GPF	RLR (48)	SIm (61)	3	7.9
Rhamnaceae	11	98	115	EM-AM, AM		2.3	GIP	1	SSB, GPF (81)		FPF (106)	1.4	4.6
Rosaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Rubiaceae	4	15	16	AM		0	GIP	1	SSB, GPF (12)	RLR (3)	FPF, SAF FAA (1), NSH (4)	1.5	2.5
Ruppiaceae	1	4	4	NM	Aqua	4	Water	4			NSH	0	3
Rutaceae	15	128	176	AM		0	GIP, SIP	1.7	SSB, GPF (141)	RLR (18)	FPF (89), SAF (4), VFF	2.1	3.8
Santalaceae	7	28	28	NM, Para		4	GIP	1.3	SSB, GPF (15)	RLR (1)	SIm (27)	1.3	6.6
Sapindaceae	3	28	36	AM		0	GIP	1	SSB, WDS, GPF?	RLR (6)	FPF (7), SIm (1)	1.3	2.3
Scrophulariaceae	6	124	170	AM		0	GIP	1.7	SSB, GPF		SAF (30), NSH (8)	0.7	2.3
Solanaceae	10	44	49	AM		0	GIP, SIP, BPB	1.3	SSB, GPF (29)	RLR (1)	FPF (30), SAF (25), NSH (35)	1.1	2.4
Stylidiaceae	2	203	221	AM		0	SIP, GIP	3	SSB, GPF (212)	RLR (6)	FPF (15), FAA (33)	2.5	5.5
Surianaceae	1	2	2	AM		0	GIP	2	SSB, GPF		FPF, NSH	2	2
Thymelaeaceae	1	46	57	AM		0	GIP	1	SSB, GPF	RLR (6)	FPF (57)	3	5
Typhaceae	1	2	2	NM (AM)	Aqua	2	Wind	2	WDS	RLR	NSH	0	4
Urticaceae	2	3	3	NM		1	Wind	2	SSB, GPF?		FAA (3)	1	4
Violaceae	1	6	10	AM		0	GIP	1	SSB, GPF	RLR	FPF	3	4
Vitaceae	1	1	1	AM		0	GIP	1		RLR	NSH	1	2
Xanthorrhoeaceae	2	10	12	AM		0	GIP, Bird	1	SSB, GPF	RLR (11), RCB (1)	FPF, VFF	3.5	4.5
Xyridaceae	1	11	11	AM		0	GIP	1	SSB, GPF	RLR	FPF	3	4
Zosteraceae	2	2	2	NM	Marine	4	Water	4			NSH	0	8
Zygophyllaceae	2	22	22	NM, N2F?	ASD	3	GIP	1	SSB, WDS, GPF?		NSH	1	5

Appendix 2. Clades of southwestern Australian plants which have exceptional diversity and highly specialised nutrition, pollination or fire traits (see Table 1 for abbreviations).

Family or group	Genera	Species WA	Subspies WA	Informal names	Taxa WA	Taxa SWAFR	Australia species	Global species	Nutrition	Pollination	Fire, etc.
Casuarinaceae	*Casuarina, Allocasuarina*	29	4	0	33	32	69	91	AM-EM, AM, CR, N2F	Wind	CSB, RSA, RLR, WDS
Eucaylptineae (Myrtaceae) with EM	Trees—*Eucalyptus, Corymbia*, etc.	389	80	26	497	309	883	~860	EM (AM)	Bird, Insect GIP, NFM	CSB, RSA, RLR, REB, GDR
Melaleuceae (Myrtaceae)	Shrubs—*Melaleuca alliance*	281	39	3	324	570	453	~500	EM-AM, AM, AM-EM	Insect GIP & Bird	CSS, some RCL
Mimosoideae (Fabaceae)	*Acacia* only	641	93	67	801	571	1058	~1550	AM, AM-EM, EM (AM), N2F	Insect GIP, NFM	SSB, some RLR
Mirbelieae (Fabaceae)	*Gastrolobium, Gompholobium*, etc.	489	20	31	540	203	405	~700	EM-AM, AM, N2F, CR	Insect SIP & Bird	SSB, RLR, SGP
Mirbelieae in part	*Daviesia* only	103	12	0	115	117	130	130	NM-CR, AM, N2F	Insect SIP & Bird	SSB, RLR, SGP
Pomaderreae (Rhamnaceae)	Australian genera	112	15	1	128	115	251	~260	EM-AM or AM	Insect GIP	SSB, RLR, SGP
Proteaceae	*Banksia, Grevillea*, etc.	758	177	32	967	930	1176	~4000	NM-CR	Bird, NFM, SIP, GIP, SPP	CSB, SSB, RLR, REB, GDR, WDS
Cyperaceae	13 genera	351	14	96	461	268	882	~5500	NM-DR, SBR	Wind	RLR, RCB (FAA), SSB, SGP, LCP
Restionaceae	19 genera	102	5	1	108	111	181	485	NM-DR, SBR	Wind	SSB, RLR, SGP, LCP
Haemodoraceae	*Haemodorum, Anigozanthos*, etc.	94	27	3	124	110	131	131	NM, SBR	Bird, SIP, GIP	RCB, RLR, SSB, SGP, FPF, WDS
Dasypogonaceae	*Dasypogon, Kingia, Calectasia*	19	0	0	19	19	20	16	NM, SBR	Insect GIP, BPB	SSB, RLR, SGP, LCP
Carnivorous plants (3 families)	Drosera, Utricularia, etc.	150	14	2	167	127	251	860	NM carnivorous	Insect GIP (1 bird)	RCB, FAD, FAA, SGP, FPF
Parasitic plants (4 families)	*Amyema, Santalum, Nuytsia, Cuscuta*, etc.	111	11	1	123	69	190	4881	NM parasites with haustoria	Bird & insect	SIm (most), bird dispersed
Orchidaceae	Terrestrial genera (26)	398	38	24	460	440	1866	~28500	Orchid mycorrhizas	SIP (most are deceived)	RCB, many FPF, some SIm, WDS
Asparagaceae	*Thysanotus* only	49	0	10	59	53	64	64	Unique mycorrhiza type	SIP, BPB	RCB or RLR, SSB, SGP
Stylidiaceae	*Stylidium, Levenhookia*	254	12	9	275	221	300	~310	AM	SIP (trigger), SPP	SSB, SGP, some RLR or RRB